Cryptogam succession in relation to forest age and log decay progression in Tasmanian wet eucalypt forest

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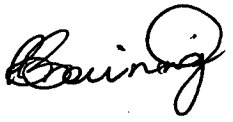

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ABSTRACT

Cryptogam communities on coarse woody debris persist in forests regenerating after the first clearfell, burn and sow harvesting rotation due to harvest residue. The habitat disturbance dynamics in a regenerating forest is different from the natural wildfire disturbance, as is the dynamics of coarse woody debris, which, while different, also provides an opportunity for new bryophyte community development. How bryophyte communities develop in response to this new system dynamic is largely unexplored. Community development may depend on time since disturbance and/or the degree of decomposition of the coarse woody debris. For individual species and communities as a whole, it is not known which of these two effects dominates or what environmental attributes affect the resulting communities. This research attempts to tease apart these issues by examining the time dependent response of cryptogamic communities growing on coarse woody debris to first rotation clearfell, burn and sow harvesting and the relative significance of forest age and log decay progression on community succession.

Subsequent to clearfelling, cryptogamic communities on coarse woody debris were compared from wet eucalypt forests of increasing age. There were significant differences in species richness and community composition between forest age and between log decay stage. Older forests were the most species rich. More individual species had significant associations with logs of intermediate decay classes than with logs of an earlier decay class. The ecology of individual species varied considerably for forest age and log decay class associations and there were distinct early, middle and late successional species identified.

Forest climate measures of temperature and vapour pressure deficit were used as an indication of the variation in large scale habitat conditions over time between forests of each age and to examine the influence of habitat conditions associated with forest age on of coarse woody debris. There were significant changes over time for temperature and vapour pressure deficit where mesoclimatic conditions became less variable as forest age increased. Log moisture was a direct measure of the fine scale habitat conditions influencing cryptogam communities of coarse woody debris, especially in relation to log decay stage. Log moisture had a significant influence on bryophyte community composition over time and was important for determining the succession of cryptogamic communities when combined with mesoclimatic conditions.

The effect of forest age and log decay stage on cryptogam communities of coarse woody debris suggests that both of these time dependent processes play an important role in community succession, and that the distinction between the two habitat variables may vary depending on time since clearfell, burn and sow disturbance. Fine scale community analysis revealed that at any forest age and at any decay stage there were significantly associated species. While this study has shed some light on how succession plays out in the first decades of the first clearfell, burn and sow rotation, it also suggests that communities follow a predominantly similar successional pathway as would occur in a forest regenerating after natural wildfire disturbance; however, it is likely that successive harvesting events based on 100 year rotations will result in the loss of some cryptogam species. Managing forests after clearfell, burn and sow for the development of mature stands and for actively facilitating the persistence of a range of decay stages and coarse woody debris habitat structures at the site and landscape levels may be appropriate, and the findings of this study are discussed in this context.

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CONTENTS

1. INTRODUCTION

Although they are important components of plant diversity in forest and other systems, the ecology of cryptogamic land plants (mosses, liverworts, hornworts and ferns) is much less well known than that of their more conspicuous relatives, the angiosperms and conifers. This thesis covers one gap in this knowledge - the nature of ecological succession on coarse woody debris in managed wet eucalypt forests of Tasmania. This will be addressed by explaining the nature of cryptogamic land plants, the relationship between floristics and macro- and micro-habitat characteristics, and the state of knowledge on succession in wet eucalypt forests, and then presenting new results that define the nature of the succession after clearfell burn and sow harvesting of wet eucalypt forests in southern Tasmania.

1.1 Cryptogam floristics

Although placed under the umbrella term of cryptogams, the mosses (Bryophyta), liverworts (Marchantiophyta), hornworts (Anthocerotophyta), lycopods (Lycophyta) and ferns (Pteridophyta; including psilophytes and sphenophytes) represent separate lineages within the plant kingdom (Goffinet *et al.* 2009). Their distinction from other land plants is that (with rare exceptions) the haploid gametophyte is the ecologically dominant phase of the alternation of generations (Crandall-Stotler *et al.* 2009; Goffinet *et al.* 2009; Renzaglia *et al.* 2009). Within the cryptogamic flora, mosses, liverworts and hornworts (collectively bryophytes) differ from ferns and lycophytes because of their lack of vascular tissues (Crandall-Stotler *et al.* 2009; Goffinet *et al.* 2009; Renzaglia *et al.* 2009). Although the groups of cryptogams are structurally and phylogenetically different, they have a similar ecological preference of habitat (Garrett 1996; Proctor 2000).

The bryophytes comprise the great bulk of cryptogamic diversity in the systems studied, and receive particular attention in this thesis. There are no lycophytes present in the current study system, so they will not be considered further.

Together, cryptogams are important components of forest ecosystems contributing to forest structure, moisture dynamics, forest humidity, nutrient cycling and providing habitat for other organisms (Turner and Pharo 2005). They make a significant contribution to plant diversity in boreal and temperate forests where they occur on a variety of substrates that may include trees, rocks, soils or decaying logs (*Cole et al.* 2008; Rudolphi 2007; Turner 2005). There are approximately 11000 ferns worldwide and 87 of these are native to Tasmania (Buchanan 2009). Worldwide, bryophytes exceed the number of ferns with

approximately 5000 liverwort species (Crandall-Stotler *et al.* 2009), 13000 moss species (Goffinet *et al.* 2009) and 150 hornwort species (Renzaglia *et al.* 2009). In Tasmania, there are approximately 450 moss species (Buck *et al.* 2002; Moscal and Kirkpatrick 1997) and 300 liverwort species (Ratkowsky 1987), although these numbers are still under revision (Dalton *et al.* 1999).

1.2 Cryptogam habitat relationships

Bryophyte distribution and abundance is largely dependent on forest and substrate climatic conditions including humidity, temperature and exposure to wind and light (Ashton 1986; Pharo and Beattie 2002). Bryophytes have a close relationship with their environment at both the macrohabitat and microhabitat scales. There is a wide range of tolerances for environmental variation among species due to most species' dependence on external water. Much of the extraordinary diversity of bryophyte morphology appears to be the result of individual species' adaptations to their environment based on external water as a primary resource.

Much of the ecological variation in bryophytes is related to their diversity of morphology. They range from various leafy to thallose arrangements mostly existing in a colonial growth form. All are small herbaceous plants which lack lignin and this difference in structure and scale to tracheophytes results in a major difference in physiology (Proctor 2000). Bryophytes are largely dependent on water present externally on the plants themselves and most bryophytes conduct water and metabolites through diffusion (Proctor 2000). Indeed these species can take up water and nutrients over the whole surface of the plant, often by means of specialised structures such as external capillary spaces around leaf bases, by thick mats of rhizoid tomentum or in channels on the leaves (Proctor 2000). The life history of the bryophyte is markedly influenced by environmental conditions as well. There is a reliance on an aquatic medium for fertilisation while spore dispersal is dependent on particularly favourable environmental conditions that vary depending on the species (Goffinet *et al.* 2009). Some species require lower humidity than is normally required to trigger the release of spores, with some species requiring wind for passive dispersal (Goffinet *et al.* 2009). Other species are more dependent on high moisture conditions and require high humidity or rain events (Goffinet *et al.* 2009).

This dependence on potentially unpredictable and highly variable external water makes bryophytes susceptible to environmental variation. Most bryophytes photosynthesise and

grow when the environment is moist and water availability is not limiting (Proctor 2000). Protection from wind and sunlight damage is important in maintaining moisture conditions suitable for plant growth and success. Temperature and heat associated with evaporation on the plants themselves caused by external sources and photosynthesis contributes to the complexity of bryophyte water relations (Proctor 2000). Growth habits of many species, such as dense mats or cushion-like forms can increase plant boundary layer protection and optimise growing conditions (Proctor 2000). Still, many bryophytes dry out in equilibrium with the surrounding environment where the water content of plant cells varies passively with external water conditions – a physiological condition called poikilohydry (Malcolm and Malcolm 2006). Poikilohydry makes desiccation tolerance essential in many bryophytes because this allows them to tolerate drought periods by shutting down metabolism when moisture conditions are unfavourable (Proctor 2000). Another benefit of desiccation is that species tolerance to extremes of temperature is increased when they are dry rather than wet (Proctor 2000). The close relationship between plant growth, reproduction and water availability means that bryophytes are highly dependent on the moisture conditions of their surrounding environment. This is why macrohabitat and microhabitat conditions are so important in determining bryophyte species distribution and abundance.

Unlike the bryophytes, ferns are vascular plants in which the sporophyte possesses well developed shoot and root structures and, therefore, have internal water and nutrient transport systems that allow them to grow larger than bryophytes and be less dependent on the surrounding environment (Raven *et al.* 1992). The gametophyte generation consists of an undifferentiated prothallus, where sexual reproduction of the ferns occur, whose survival is dependent on suitable microenvironmental conditions (Raven *et al.* 1992).

1.3 Cryptogam habitats

Diversity in forest ecosystems is influenced by many habitat factors, at both the macrohabitat and microhabitat levels (Pharo and Beattie 2002; Vitt and Belland 1997). Macrohabitat and microhabitat variation increases habitat diversity and has been shown to determine extensive cryptogamic diversity through a complex forest landscape with an abundance of different habitats (Pharo and Beattie 2002; Turner and Pharo 2005). The variation in microhabitats is particularly important for cryptogam species diversity because many species have specific habitat preferences within general habitat types (e.g. forest).

This is determined by their suitability to particular environmental conditions and their capacity to tolerate variations in these conditions (Catcheside 1980).

Within general habitats there are microhabitats which include various substrate types. Cryptogam species are often classified into functional groups based on substrate preferences. These include epiphytic, terrestrial, epilithic, epiphyllous and epixylic cryptogams (Ashton 1986). A diversity of microhabitats will allow for a wide range of species preferences and encourage species diversity.

Epiphytic bryophytes and ferns grow on stems, trunks and branches of living vascular species and are most abundant in moist areas (Bates 2000). Epiphytes often have a high degree of host specificity because of their susceptibility to environmental variation on these relatively exposed substrates. Jarman and Kantvilas (2001), in a study on the understorey habitats in Tasmanian wet eucalypt forests, found that diversity of bryophytes on trunks of *Eucalyptus obliqua* was dependent on bark thickness and texture. This is consistent with a study by Ashton (1986) on the ecology of various bryophyte communities in *Eucalyptus regnans* forests in Victoria. Ashton (1986) found that different bryophyte communities were present on trees with different bark types and on trees of different ages. This was because, as a tree ages, the bark thickens and is more water retentive, which in turn buffers species from humidity fluctuations in the surrounding forest environment. Jarman and Kantvilas (2001) found that epixylic bryophyte communities were less abundant with distance from the ground, indicating a close relationship with the surrounding environment where conditions close to the ground are more favourable for growth on a substrate with little water holding capacity.

Jarman and Kantvilas (2001) found that terrestrial bryophyte distribution on soils was dependent on the density of the surrounding vascular plant species, the amount of accumulated litter on the soil surface and the effect of the chemical composition of this litter on the soil substrate. These habitat conditions either reduce substrate availability or make substrate patches unsuitable for bryophyte growth. Ashton (1986) also found that bryophytes were affected negatively by litter accumulation, being most abundant on sloping areas where there was less litter.

Epiliths inhabit rocks and boulders where the size and contour of the substrate is important for species abundance and distribution (Ashton 1986; Bates 2000). Ashton (1986) found

that the slope of the rock determined the amount of litter accumulation and therefore the degree of inhibition of bryophyte growth.

Epiphyllous bryophytes are those that grow on the leaves of other plants, occurring in moist habitats with consistently humid environments (Bates 2000). Most are small short-lived species including mainly specialist liverwort species though there are also many facultative epiphyllous mosses (Bates 2000).

Of particular interest to the present study are epixylic species, which occur on logs and other woody debris (Bates 2000). The quality of a log is important in determining community composition and abundance. Crites and Dale (1998), in a study on epixylic communities in relation to characteristics of the substrate, found that species tend to colonise the log once decay has progressed from its early stages where bark is still present, and that communities were more abundant on logs in advanced stages of decay and of large diameter. These logs provided a greater array of suitable substrate patches than smaller and less decayed logs. On a macrohabitat scale, the diversity and structural complexity of habitats contributes to the abundance and quality of potentially suitable substrates. This in turn provides a diversity of habitats within and between substrate types that allow for the occurrence of a diversity of species from a variety of functional groups.

1.4 Macrohabitats and microhabitats in forests

Forest structural complexity is the combination of one or more forest structural attributes and their spatial arrangement (Lindenmayer *et al.* 2002). This structural complexity is an important foundation for species diversity because it provides a variety of microhabitats and substrates for a wider range of species to occur (Lindenmayer *et al.* 2002). Structural attributes include the range of substrates, ground cover, understorey and overstorey vascular plants (Lindenmayer *et al.* 2002).

Vascular plants create the large scale structure of the forest and have a direct affect on the surrounding environment (Ashton 1986). As the forest structure changes over time, largely due to changes in the vascular community, so does the nature of the forest microclimate (Kantvilas and Jarman 2004). Forest age partly determines the composition of the vascular community and, consequently, important ecological factors including canopy cover, microclimate and forest structural diversity (Kantvilas and Jarman 2004). Because of this, different vascular plant communities may be expected to have different associated bryophyte flora. A diverse forest landscape has a wide variety of cryptogam communities

due to different environmental attributes and species interactions with this environment (Ashton 1986; Hylander *et al.* 2002). Crites and Dale (1998) found that bryophyte communities were different between forest ages in boreal forests suggesting that time and associated time-dependent forest variables such as structure and substrate heterogeneity were important influences on bryophyte community composition. Pharo and Beattie (2002) found that time since fire was important in determining bryophyte community composition, presumably because of the development of vascular communities in the surrounding forest and its increasing structural complexity.

Habitat heterogeneity is the variation in habitat types and is largely a function of forest age and substrate diversity, both within a substrate type and between substrate types (Cooper-Ellis 1998; Kantvilas and Jarman 2004; Lindenmayer *et al.* 1999; Newmaster *et al.* 2003; Rambo and Muir 1998; Turner *et al.* 2006; Turner and Pharo 2005). Many substrate types contribute to the structural complexity of a forest and allow for a range of microhabitats for forest organisms. Cryptogam diversity and abundance is directly related to the quality of the substrate and whether it provides a suitable habitat (Pharo and Beattie 2002; Turner and Pharo 2005). Pharo and Beattie (2002), in a study of species diversity in Tasmanian wet eucalypt forests, found that species composition of bryophytes was related more to substrate type (microclimate) rather than site type (macroclimate). If the abundance of substrates is high, it is more likely that a wider range of microhabitats will be available to accommodate a wide variety of species' specific substrate preferences. Turner *et al.* (2006), in a study on bryophyte relationships with environmental and structural variables in old growth temperate forests, found that a high abundance of substrates was important for species diversity and determining bryophyte community assemblages.

1.5 Coarse woody debris

Coarse woody debris is a generic term covering logs and other macroscopic fragments of wood (Woldendorp *et al.* 2005). The fragments can range in size from smaller stems and branches down to approximately 10 cm in diameter up to logs that are metres in diameter and tens of metres long (Ashton 1986; Woldendorp *et al.* 2005). Coarse woody debris also includes material at all states of decay, ranging along a continuum of decomposition from freshly fallen logs to material so decayed that it is virtually unrecognisable as wood. These are often categorised into 'decay stages' that indicate the relative amount of decay and vary from logs of decay stage one, with virtually no decay, up to decay stage five, which consists of logs that are almost completely decomposed (Grove *et al.* 2002). Logs can take

many decades to reach advanced stages of decay depending on the climatic conditions of an area (Crites and Dale 1998; Söderström 1988a), with higher temperatures and moist conditions known to increase the rate of decay (Crites and Dale 1998; Söderström 1988a). Coarse woody debris can provide a diverse range of microhabitats, and is among the most important substrates for the diversity of forest organisms, influencing species composition and functioning as a nutrient resource. This substrate provides essential habitat for wood-inhabiting fungi and saproxylic beetles, as well as a substrate for a wide range of organisms that include bryophytes, lichens, ferns, birds and shelter for mammals (Harmon *et al.* 1986; Heilmann-Clausen *et al.* 2005; Lindenmayer *et al.* 1999; Pharo and Blanks 2000).

Coarse woody debris encompasses a variety of dead forest biomass including dead branches, fallen trees and stumps, which are important structural components of forest ecosystems (Sturtevant *et al.* 1997; Woldendorp *et al.* 2005). Logs are important in many ecological and physical processes such as nutrient cycling, moisture retention and carbon storage (Banks and Bennett 2003; Harmon *et al.* 1986; Sturtevant *et al.* 1997). As a temporary substrate that undergoes the process of decay, coarse woody debris alters over time (Söderström 1988b). In a natural system, the continual recruitment of new logs from falling trees and log decay progression provides a constant supply of wood in a variety of conditions (Söderström 1988b).

The amount and quality of coarse woody debris in a forest is dependent on disturbance history and the structural dynamics of a particular stand of forest (Woldendorp *et al.* 2005). Material can be added or removed by disturbances such as wildfire, windthrow and timber harvesting (Woldendorp *et al.* 2005). Variation in coarse woody debris is important for maintaining rich cryptogam communities that require logs in various stages of decay, with large logs in more advanced stages of decay supporting the most diverse communities (McAlister 1995; Pharo and Beattie 2002; Rambo 2001; Söderström 1988b). Cryptogam vegetation on coarse woody debris varies with moisture content of the wood which is closely linked with decay stage (Andersson and Hytteborn 1991). Many stages of decay may be observed on a log which contributes to the ability of this substrate to accommodate variation in species preferences for particular microhabitats (Grove *et al.* 2002). This allows many different species to occur on any given log and, consequently, in one forest area, therefore increasing forest diversity (Sturtevant *et al.* 1997). Coarse woody debris in temperate forests is one of the substrates with the greatest number of associated bryophytes

(Grove *et al.* 2002). Approximately 165 species are known to occur on logs in southern Tasmanian wet sclerophyll forests (Grove *et al.* 2002), although it is plausible that this number will increase with greater knowledge. Jarman and Kantvilas (2001), in a study on the diversity of bryophytes in wet eucalypt forest in relation to substrate type, recorded 59 bryophyte species on *Eucalyptus obliqua* logs, which made up a significant proportion of the bryophyte flora in these forests. Turner *et al.* (2005), in a study of a similar forest type in Tasmania, found that many of the species that make up the abundant bryophyte flora in these forests are specifically associated with a particular substrate type, and that this can be influenced by the age of a forest.

1.6 Forest succession

Succession theory forms one of the foundations of modern ecology and conservation biology, and is crucial for the understanding of how an ecosystem responds to forest disturbance such as timber harvesting, as well as to the patterns and processes linked to forest regeneration (Rudolphi 2007). The classic view of succession is the predictable accumulation and replacement of species assemblages over time, beginning with colonising species and finishing with the development of a community of species that are characteristic of mature vegetation (Clements 1916). This theory was built upon by Egler (1954) in describing initial floristic composition, and how succession is driven by individual species attributes as well as community interactions. This initial floristic view of succession is based on the influence of propagules from the pre-disturbance vegetation and initial species immigration that determine the starting point of succession and, therefore, through differences in colonisation, growth and competition, determine the successional pathway that follows (Egler 1954). Species accumulation, however, may not be predictable if it is the passive cumulative immigration of species over time, which is based on random chance. This is part of the theory of species acting independently, making community composition the result of chance dispersal rather than succession (Gleason 1926).

These theories of succession are based on a linear view of community development and, as such, lack the inherent complexity of real forest ecosystem processes (Taylor *et al.* 2009). What must to be taken into account is the added effects of environmental variation in time and space that are linked to ongoing disturbance regimes (Taylor *et al.* 2009). The multiple pathway approach to succession theory takes into account departures from expected pathways that were based on limited earlier linear successional theories (Taylor *et al.* 2009). Succession is multi-dimensional and involves multiple pathways and mechanisms

(Taylor *et al.* 2009). In this multiple pathway approach to succession, the pathway is the replacement of species assemblages and accumulation of species over time. Mechanisms include other environmental attributes and species specific interactions (e.g. time, scale, disturbance, species' attributes and life history traits) that drive successional pathways (Taylor *et al.* 2009). The combination of these provides models of predictable successional pathways that describe the relationships between mechanisms and various successional stages and take into account what may have been considered departures from predicted community development based on the classical views of succession (Taylor *et al.* 2009).

1.7 Cryptogamic land plant succession on coarse woody debris

Multiple pathway models describe forest succession through species attributes, community dynamics, environmental conditions, the type of disturbance and time since disturbance (Taylor *et al.* 2009). The effect of forest succession on cryptogam communities has been described in numerous studies. Botting and Freeden (2006) found that the microclimate in young forests was not suitable for the growth of most liverwort species due to the low water availability, low humidity and greater temperatures than occurs in more suitable habitats in older forests. Hylander *et al.* (2002) found that bryophyte assemblages were directly related to evaporation, where habitats protected from exposure to high intensity sunlight and desiccating winds maintained a consistently humid environment likely to promote not only species diversity, but also the growth and vigour of the bryophyte community.

Succession on logs can be described with the inclusion of ongoing disturbance and accounts for the variation in species assemblages brought about by microhabitat variation on the scale of a single substrate patch (Ashton 1986). Coarse woody debris is one of the limited numbers of substrates that show a distinct case of succession (Söderström 1988a). Decay causes many changes in the coarse woody debris substrate and each decay stage may be more suited to a particular suite of species. This process of continual disturbance means there is a continual successional replacement of species (Söderström 1988a). Söderström (1988a) described coarse woody debris as being a transitory substrate that changes during its lifetime, with the main changes that affect the substrate being the loss of bark and changes in wood texture that are directly related to decay stage. The texture of a log affects community succession because of increased colonisation rates with increasingly rough surfaces and moisture holding capacity (Söderström 1988a).

Of particular relevance to this study is the concept of scales in succession – the forest (macrohabitat) scale and the substrate (microhabitat) scale. The combination of the effect of two successional scales cannot be overlooked. Crites and Dale (1998) found that species assemblages of cryptogams on particular decay classes were different and, also, that assemblages for each decay class varied with forest age. They speculated that as well as time being important, forest structural attributes had an overall effect on community assemblages. Ashton (1986) found that the rate of succession occurring on logs is based on the moisture conditions of the surrounding forest, with increased rates of succession on logs in more moist areas. This also could be related to the process of decay, the rate of which is largely influenced by moisture conditions (Söderström 1988a).

Different scales of succession are also important in predicting the effects of disturbance on communities. Ryömä and Lakka-Lindberg (2005) found that allowing for an increase in coarse woody debris after restoration treatments following forest harvesting would promote the long term persistence of epixylic species in the landscape. They show that implementing management strategies for a desired outcome requires the ability to predict the forest successional pathway on many scales. Multiple pathway models of succession can provide predictions of future conditions when paired with extensive, accurate ecological information (Taylor *et al.* 2009) and will result in forest management policies with improved relevance, application and results (Ryömä and Laaka-Lindberg 2005).

1.8 Tasmanian forests

Tasmanian forest is classified as Austral Montane Forest, Temperate Rainforest, Wet Sclerophyll and Dry Sclerophyll Forest (Jackson 1999). Varying rainfall, temperature, geology and topography across the state as well as different fire intervals alter communities and result in a floristic mosaic of Wet Sclerophyll Forests in the Tasmanian landscape (Jackson 1999). Wet eucalypt forests are one of the major forest communities and are among the most important habitat types for plant and animal diversity.

Wet eucalypt forests cover nearly half of Tasmania and include both wet sclerophyll and mixed forest types. Although both these forest types have emergent eucalypts, often of the same species, they differ in the canopy and understorey composition. Wet sclerophyll has a layer of tall broad-leaved shrubs, with ferns dominating the lower strata, whereas mixed forests have rainforest species as a major understorey component (Wells and Hickey 1999). Wet eucalypt forests develop in areas of high rainfall in excess of 1000 mm per annum and

where there is a low fire frequency; however, fire is key to the maintenance of these forests (Wells and Hickey 1999). Without fire every 20 - 100 years for wet sclerophyll forest, this community would succeed to mixed forest as rainforest understorey species replace the wet sclerophyll understorey. In turn, if mixed forest remains unburnt for more than approximately 350 years, this forest will be replaced by rainforest though the death of the dominant eucalypt component (Wells and Hickey 1999).

Locally, it also has been recognised that bryophytes follow a successional sequence in wet eucalypt forests (Turner 2003); however, past studies have concentrated on one successional stage or a wide variety of substrates and only recently have studies begun to identify the complete successional pattern of cryptogams on logs (Ashton 1986; Duncan and Dalton 1982; Jarman and Kantvilas 2001; Turner 2003). Where information is available, it appears that there are predominantly similar species assemblages, but it is the relative differences in species occurrences over time within these assemblages that define successional patterns between forest types and forest ages.

1.9 Management practices and impacts on coarse woody debris

In Tasmania, wet eucalypt forests have been exploited for their hardwood timber resource since the 1820s (Wells and Hickey 1999). Since then, timber harvesting has grown into a significant component of Tasmania's economy. It has progressed from selective harvesting to clearfell, burn and sow harvesting, which has been the main harvesting method since the 1960s when the market for timber and pulpwood for paper manufacturing expanded and the exportation of woodchips began (Hickey *et al.* 2001; Turner 2003; Wells and Hickey 1999). This harvesting technique involves removing all trees in an area and then creating a suitable seed bed for regeneration by using a high intensity burn to remove the dense understorey vegetation and other harvesting debris (Hickey *et al.* 2001). High intensity burns are used to mimic a natural wildfire event which stimulates regeneration in a natural forest disturbance regime in these forests (Turner 2003). The suitability of this technique and impact on wet eucalypt forest biodiversity and structure is still being questioned even with its substantial use over the last four decades (Turner 2003).

Forest harvesting modifies a forest area dramatically and consequently brings about many changes that affect the original forest ecosystem, such as increased light at levels beyond the original canopy, reduced site moisture and lower humidity, simplified macrohabitat structure, microclimates with increased variation in conditions and reduced availability of

substrates (Botting and Fredeen 2006; Newmaster and Bell 2002; Newmaster *et al.* 2003). This alteration to the forest environment, particularly the effects on substrate availability are of increasing concern in Tasmanian wet eucalypt forests because of the subsequent effects on communities (Grove *et al.* 2002; Hickey *et al.* 2001; Pharo and Blanks 2000). The number of suitable habitats decreases after harvesting, consequently decreasing forest bryophyte species diversity by reducing available habitat to suit particular species habitat preferences (Newmaster and Bell 2002; Newmaster *et al.* 2003; Söderström 1988a; Söderström 1988b). This, coupled with other direct changes to microclimate, such as reduced humidity and increased exposure, results in conditions unsuitable for bryophytes (Botting and Fredeen 2006).

Coarse woody debris is of particular interest because of its importance for biodiversity of Tasmanian wet eucalypt forest and its susceptibility to substantial negative impacts brought about by forest harvesting (Grove *et al.* 2002). Pharo and Beattie (2002) found that while time since fires was a significant variable in determining bryophyte community composition on all substrates, logging was not significantly correlated with most substrates. In their study, logging was found to have significant impacts on bryophyte communities on coarse woody debris only where time since logging had significant effects on the amount of logs in advanced stages of decay. Many studies have highlighted the impact of harvesting on coarse woody debris heterogeneity, abundance and subsequent recruitment worldwide (Andersson and Hytteborn 1991; Meggs 1996; Ódor and Standovár 2001; Rambo and Muir 1998). The pattern of coarse woody debris in managed forests includes a large input of logs at the time of harvesting, especially after the first logging rotation, but a decrease in accumulation in the longer term (Meggs 1996). The regenerating forest will contribute little in the way of dead wood as there are no old or dying trees contributing to coarse woody debris accumulation as seen in natural stands (Grove *et al.* 2002; Sturtevant *et al.* 1997; Turner and Pharo 2005). Loss of this structural diversity in the form of substrate heterogeneity may have significant impacts on associated biodiversity (Lindenmayer *et al.* 2002).

Knowledge of the responses of forest organisms to disturbance is essential for understanding ecosystem stability and dynamics and contributing to better informed management (Åström *et al.* 2007). It is important to get an in depth understanding of the forest landscape focusing on coarse woody debris, as it is one of the most important substrates for forest biodiversity. Knowing the patterns of bryophyte diversity in relation to

the regenerating forest habitat will provide an opportunity to minimise the impact of forest operations on biodiversity by informing managers of the probable implications of forest management plans and practices (Newmaster *et al.* 2003; Pharo and Blanks 2000).

1.10 This thesis

The present study examines regeneration of cryptogamic communities on coarse woody debris in wet eucalypt forests of southern Tasmania at the macrohabitat and microhabitat scales. The study aims to determine whether log decay and forest age each influence community succession in forests regenerating after clearfell, burn and sow harvesting. Both forest age and log decay directly influence habitat conditions and contribute significantly to the nature of associated plant communities. This study concentrates on three main hypotheses which are important for general understanding of cryptogamic community succession on coarse woody debris and determining focus of effective forest management: (1) there is a succession pattern on coarse woody debris after clearfell burn and sow and (a) this involves an overall increase in diversity; and (b) there are early, mid and late successional specialists; (2) forest age and log decay have significant independent effects on cryptogam community succession; (3) mesoclimate becomes less variable and more hospitable for cryptogams with increasing forest age, and log moisture increases with the extent of log decay and; (4) these changes can be associated with cryptogam community succession.

Finally, these results will be compared with previously collected data from 'natural' post-fire regeneration in the same region to assess the similarity of post-logging and post-fire communities at the same age (43 years), as well as to compare these with naturally generated old growth communities. This will provide insight into the effects of clearfell, burn and sow harvesting on coarse woody debris communities to help assess the impacts that this harvesting method might have on regenerating biodiversity in the long term. This information will assist in the development of effective forest management of coarse woody debris that will result in the desired long term objectives of balancing biodiversity and resource management for forest sustainability.

2. METHODS

2.1 Study sites

Data on the bryophytes and ferns growing on coarse woody debris were collected from 16 sites in the Warra Long Term Ecological Research site (http://www.warra.com/warra/about.html) and nearby areas in the Arve Valley, Southern Tasmania (Figure 2.1). The Warra research site was established by Forestry Tasmania to facilitate the understanding of ecological processes of Tasmania's wet eucalypt forests, specifically *Eucalyptus obliqua* forests. This land area is partly within the Tasmanian Wilderness World Heritage Area, which is managed for conservation values, and partly within State forest, which is managed for multiple uses including wood production.

Table 2.1. Details of study sites.

Site	Abbreviation	Forest age (years)	Latitude (S)	Longitude (E)	Altitude (m)	Transect length (m)	Basal area (m^2/ha)
HP002C	HP	8	43°14'54"	146°57'16"	250	111	8
PC085B	PC	8	42°08'16"	146°42'13"	150	79	0
WR008B	WB	8	43°05'42"	146°41'35"	150	56	0
WR008H	WH	8	43°05'47"	146°41'06"	150	34	2
EP079D	ED	20	43°14'17"	146°51'19"	550	101	58
EP082B	EB	20	43°14'9"	146°53'12"	600	63	12
WR009A	WA	20	43°05'23"	146°40'20"	200	51	20
WR012E	WE	20	43°02'47"	146°41'57"	450	85	0
AR048H	AH	32	43°06'25"	146°45'57"	350	83	34
KD009J	KD	32	43°10'48"	146°52'09"	200	170	22
WR004G	WG	32	43°04'9"	146°43'00"	200	114	26
WR007C	WC	32	43°05'17"	146°42'32"	200	61	46
AR014E	AE	43	43°09'34"	146°48'14"	200	66	46
AR051F	AF	43	43°07'06"	146°47'15"	450	188	38
AR064I	AI	43	43°06'56"	146°50'42"	200	129	38
AR070I	AR	43	43°05'19"	146°48'30"	150	117	26

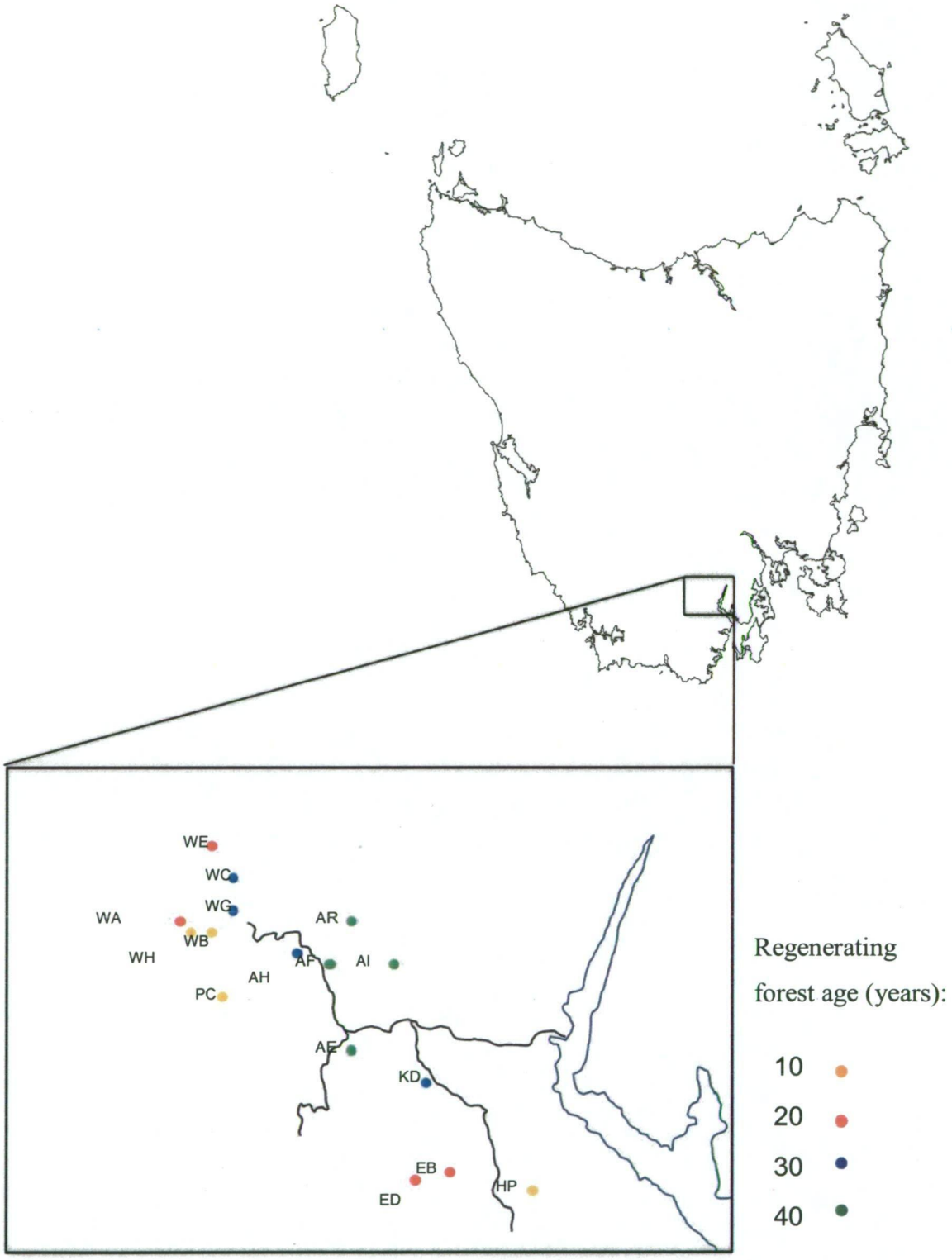

Figure 2.1. Map of Arve River area in Tasmania showing the location of all field sites. Sites are labelled according to the abbreviations in Table 2.1

2.2. 8 year old regenerating forest.

2.3. 20 year old regenerating forest.

2.4. 32 year old regenerating forest.

2.5. 43 year old regenerating forest.

Figures 2.2 - 2.5. Examples of each regeneration stage of wet eucalypt forest after clearfell, burn and sow for each regenerating forest age used in this study. Dataloggers are shown in their protective covers.

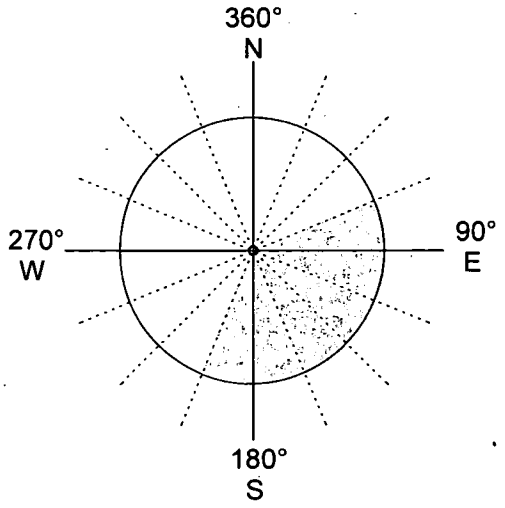

Figure 2.6. Aspect grouped into 5 classes (1 = northwest, 2 = north or west, 3 = northeast or southwest, 4 = east or south, 5 = southeast). This is as determined by (Kirkpatrick and Nunez 1980) in a study researching aspect driven vegetation conditions in Tasmanian eucalypt forest vegetation. Only those sites occurring within the shaded aspect were assessed.

A chronosequence-type approach (Crites and Dale 1998) was followed in this study because of the impracticality of directly tracking changes over the successional time sequence. This involved selecting sites of different times since logging, and ensuring that these sites were as closely matched as possible in all other characteristics except time since disturbance. Four sites were sampled from each of four ages of forest regenerating following clearfell, burn and sow in the years 1966 (43 years ± 1 year), 1977 (32 years ± 1 year), 1989 (20 years ± 1 year) and 2001 (8 years ± 1 year) (Figures 2.2 – 2.5). All sites were characterised by wet eucalypt forest dominated by *Eucalyptus obliqua*, had soils overlying Jurassic dolerite, and a southerly aspect as defined in Figure 2.6 (Table 2.1). Basal area of *Eucalyptus obliqua* was calculated for each site using a prism wedge with a factor of 2 (Table 2.1). The monthly temperature at Warra for the 12 month period from April 2008 until March 2009 ranged from a mean maximum of 18.9°C in February to mean minimum of 1.3°C in July, and the monthly rainfall ranged from 64 mm in May to 286 mm in September (BoM 2009).

2.2 Data collection

At each site, a single transect was used for log sampling, and each log was sampled where it was intercepted by the transect. This transect started at the first log encountered at least 30 m from an edge and initially ran perpendicular to the coupe edge. The transect then

turned at right angles, alternating left and right, every 50 m until 10 logs of decay class 3 (see Table 2.2) were sampled. Logs sampled were generated in the clearfell, burn and sow harvesting event. Decay stage (Table 2.2) was assessed at the point of intersection with the transect. This method provided a representative sample of less common decay classes in each different regenerating forest age, and allowed determination of the relative frequency of logs in each decay stage.

Table 2.2. Decay classes (Woldendorp *et al.* 2002).

Decay class	Characteristics
1	Most of the bark is present
	Branches retain twigs
	Wood solid
	Wood fresh
	Wood retains original colour
2	Some bark may be present
	Twigs absent
	Decay beginning to occur but wood still solid
	Invading roots are absent
3	Bark is generally absent
	Log still supports own weight
	More extensive decay but structurally sound
	Moss, herbs, fungal bodies may be present
	Some invading roots may be present
4	Log can't support own weight
	Kicked log will cleave into pieces or can be crushed
	May be partially solid or some large chunks still remain
	Bark absent
	Small soft blocky pieces
	Branch stubs rotted down, can be removed by hand
	Moss, herbs, fungal bodies may be present
	Invading roots (when present) are throughout
5	Soft and powdery (when dry), often just a mound
	Log does not support own weight
	Does not hold its original shape, flattened and spread out on ground
	Moss, herbs, fungal bodies may be present
	Invading roots (when present) are throughout

On each log, the cover of each bryophyte and fern species were scored using modified Braun-Blanquet classes of percentage cover (1 = rare, 2 = <1%, 3 = 1-5%, 4 = 6-25%, 5 = 26-50%, 6 = 51-75%, 7 = 76-100%). This percentage cover was within the exposed area from the entire circumference of the log, 50 cm in either direction along the length of the

log from the point of intersection with the transect. Log diameter also was recorded at the point of intersection.

2.2.1 Species identification

Bryophytes and ferns were identified to species level in the field where possible. Confirmation of species was undertaken in the laboratory based on current literature using both stereo and compound light microscopes and verified with samples held at the Tasmanian Herbarium (HO) and in collections held in the School of Plant Science, University of Tasmania. Nomenclature follows McCarthy (2003) for liverworts, Streimann (2002) for mosses and McCarthy (1998) for ferns. Voucher specimens of all observed bryophyte species were lodged in the School of Plant Science, University of Tasmania.

2.2.2 Climate data

Climate data of the forest habitat was recorded using HOBOware Pro v2 Dataloggers that recorded temperature and humidity. Vapour pressure deficit was calculated from temperature and humidity data following (von Caemmerer and Farquhar 1981). Vapour pressure deficit reflects the strength of the driving force for evaporation, and is therefore directly related to the water relations of plants. As a result, we used vapour pressure deficit to reflect the likely impacts of atmospheric water status on species' potential distribution and abundance. Each datalogger was mounted on a stake 50 cm above the ground in a place where there was a 30 cm radius of space around the datalogger within 5 m of the fifth log of each transect (Figures 2.2-2.5). Each datalogger was placed within a protective cover made from a 12 cm length of standard 10 cm diameter white PVC plumbing pipe with a fitted white PVC cap. The datalogger was placed so that the sensor was suspended in free air 1 cm above the bottom of the protective cover. Data was recorded every 30 minutes from19th July 2008 until 20th March 2009. The data was divided into five "miniseasons" of equal length. Miniseason 1 was winter (19th July 2008 – 5th September 2008), miniseason 2 was early spring (6th September 2008 – 24th October 2008), miniseason 3 was late spring (25th October 2008 – 12th December 2008), miniseason 4 was summer (13th December 2008 – 30th January 2009) and miniseason 5 was autumn (31st January 2009 – 20th March 2009).

Fine scale microclimate data was collected for each log on two different periods. The first period was between the 2nd and 4th of March 2009 and the second was between the 23rd and 25th of March 2009. The week prior to the first collection dates had a mean minimum

temperature of 8.9 °C, a mean maximum temperature of 19.1 °C and total rainfall of 60mm. The week prior to the second collection dates had a mean minimum temperature of 8.1 °C, a mean maximum temperature of 17.8 °C and total rainfall of 12mm. Log moisture was measured using TESTO 606-2 Material Moisture probes set to material "2" (wood). Log moisture was recorded at the top, east and west side of each log at the point of intersection of the transect. Each wood moisture meter reading recorded moisture 2 - 5mm into the log material (depending on the hardness of the wood) by electrical resistance with a resolution of 0.01%.

2.3 Data analysis

2.3.1 Species accumulation curves

Species accumulation curves were calculated as an indication of the effectiveness of the sampling intensity used in the present study (a minimum of 10 logs of decay class 3 at each site) in representing total site diversity. To calculate species accumulation curves a log was randomly selected within a site and the species counted, then the species count of another log was added to the first log count, until all logs at a site were included in the total. This gave numbers of species found on 1 to n logs. This was repeated statistically 100 times for each site and averages were calculated.

Species accumulation was highest between logs one and three (Figure 2.7 – 2.10), but continued to increase to at least ten logs in all sites. Overall, the curves indicate a lessening of the accumulation of species with each log sampled. The rate of continuing increase at 10 logs was generally greatest in sites with high apparent species richness (especially the 32 and 43 year old sites, but also 20 year old site EP079D) (Figure 2.8 – 2.10). Thus, although extra sampling effort at any of the sites was likely to reveal more species, the resulting bias was a conservative one - real differences in diversity between age classes were only likely to be larger than those indicated from the data collected here.

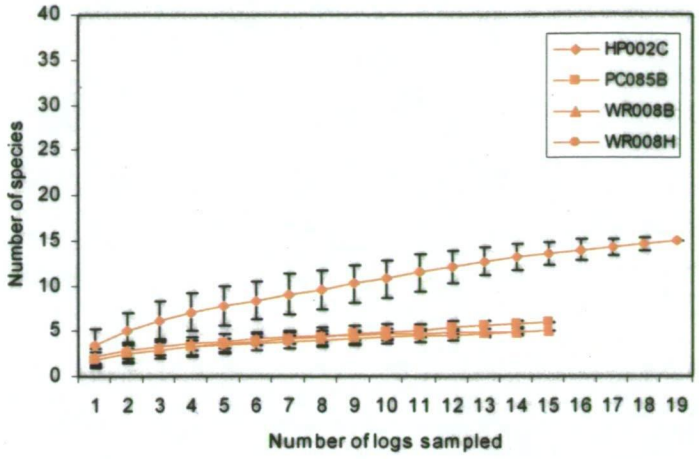

Figure 2.7. Species accumulation curves for the replicates of the regenerating forest aged 8 years

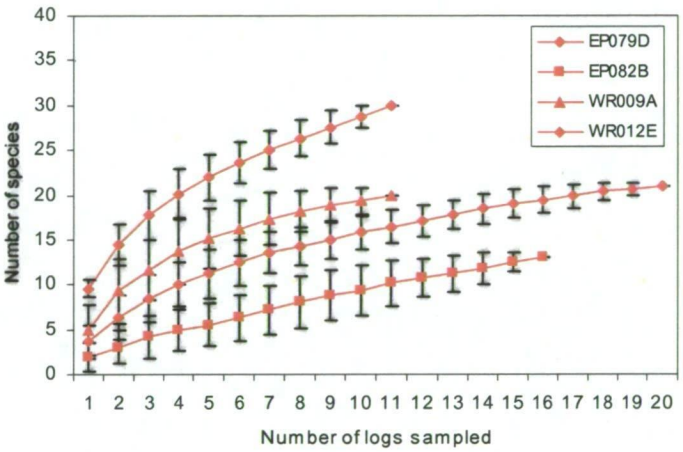

Figure 2.8. Species accumulation curves for the replicates of the regenerating forest aged 20 years

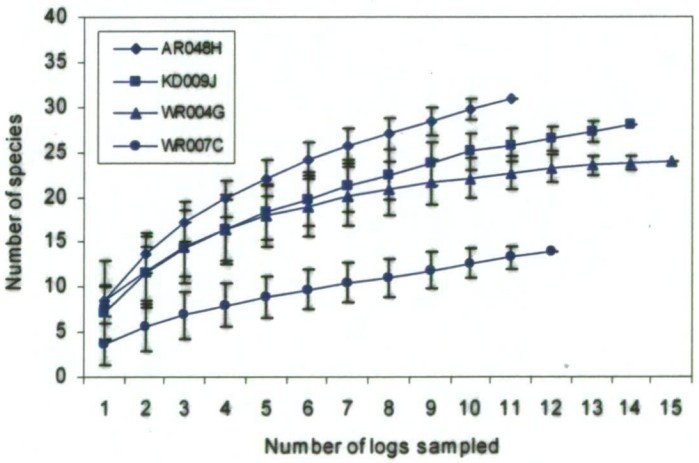

Figure 2.9. Species accumulation curves for the replicates of the regenerating forest aged 32 years

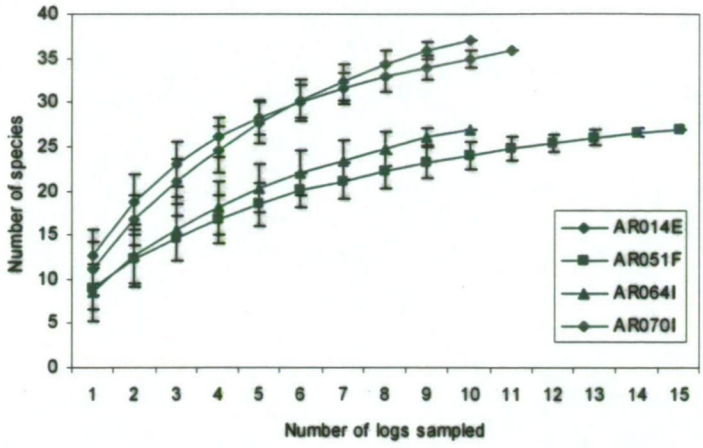

Figure 2.10. Species accumulation curves for the replicates of the regenerating forest aged 43 years

2.3.2 Segregating the effects of decay class and regenerating forest age

Sampling of bryophyte communities on logs that included decay class distributions was designed to be representative of what was present in regenerating forests. Thus analyses of this primary data set were used to assess and test general community differences among all regenerating forest ages. The primary dataset represents what was actually present in forests of different ages.

However, this primary data set was unbalanced in the number of logs sampled at each site per decay class, and in the total number of logs sampled per site and per regenerating forest age. It would have been unrealistic to expect a balanced design for this research because of the nature of the wet eucalypt forests and the changes the forest undergoes over time following clearfell, burn and sow regeneration. Some decay stages are more commonly found in some regenerating forest ages than others due to the time dependent nature of the progression of decay and regenerating forest age. Logs in lesser stages of decay are likely to be more common in younger regenerating forests and logs with more advanced stages of decay are likely to be more common in older regenerating forests (Meggs 1996). Data from the distribution of log decay classes in forests of ages up to 43 years showed that over 90% of the logs found in the 8 year age class were decay class 2, approximately equal numbers of decay class 2 and 3 were found in the 20 year age class, logs mostly of decay class 3 with some of decay class 2, 4 and 5 were found in the 32 year age class and predominantly logs of decay class 3 were found in the 43 year age class (Table 2.3). Decay class 4 logs

were uncommon in sites of all age classes, decay class 5 logs were only found in the 32 year old sites and decay class 2 logs were not found at any of the 43 year old sites.

To overcome this imbalance, two subsets of the primary data were used to assess and test either regenerating forest age or decay class as independent variables. The secondary dataset used to assess and test for the effect of regenerating forest age independent of decay class included data from the 20, 32 and 43 year age classes and logs only of decay class 3. The secondary dataset used to assess and test for the effect of decay class independent of regenerating forest age included data from decay classes 2 and 3 in only the 20 year old regenerating forest.

Table. 2.3: Total number of logs in each decay classes surveyed across the four regenerating forest ages.

	Log decay class			
Regenerating forest age	2	3	4	5
8	60 (27.2%)	2 (0.9%)	2 (0.9%)	0 (0%)
20	25 (11.3 %)	31 (14%)	2 (0.9%)	0 (0%)
32	5 (2.3%)	39 (17.7%)	5 (2.6%)	3 (1.3%)
43	0 (0%)	40 (18.2%)	6 (2.7%)	0 (0%)

2.3.3 Analysis of climate data

Although the sensors were surrounded in white protective covers, the open nature of the regenerating forest meant that in the two sites WR008B and WR004G the covers were exposed to periods of direct sunlight at or near solar midday. Preliminary analysis of data from these loggers indicated that they produced anomalously high maximum temperatures during summer. These maxima were typically many degrees warmer than more sheltered sites, and were characterised by rapid increases in temperature near solar midday, followed by relatively rapid decreases. This was interpreted as indicating that the PVC covers were acting as miniature greenhouses, and that the temperatures measurements were in error.

To correct for this, temperature and vapour pressure deficit occurring at 4 pm (solar time) will be used as proxies for maximum temperature and vapour pressure deficit. Field measurement of the horizon created by the surrounding vegetation combined with sun angles (http://susdesign.com/sunangle/) indicated that at 4pm the logger covers would have been in shade for at least 30 minutes on every day of the year. Temperature and vapour

pressure deficit at 4pm were strong predictors of maximum daily temperature and 4pm daily vapour pressure deficit in the 14 sites where exposure to direct sun was not a problem (Figure 2.8 and 2.9). To eliminate the effect of any remaining outlying values the 90th percentiles of 4pm temperature and vapour pressure deficit and 10th percentile of minimum temperatures and vapour pressure deficit readings will be used throughout this thesis.

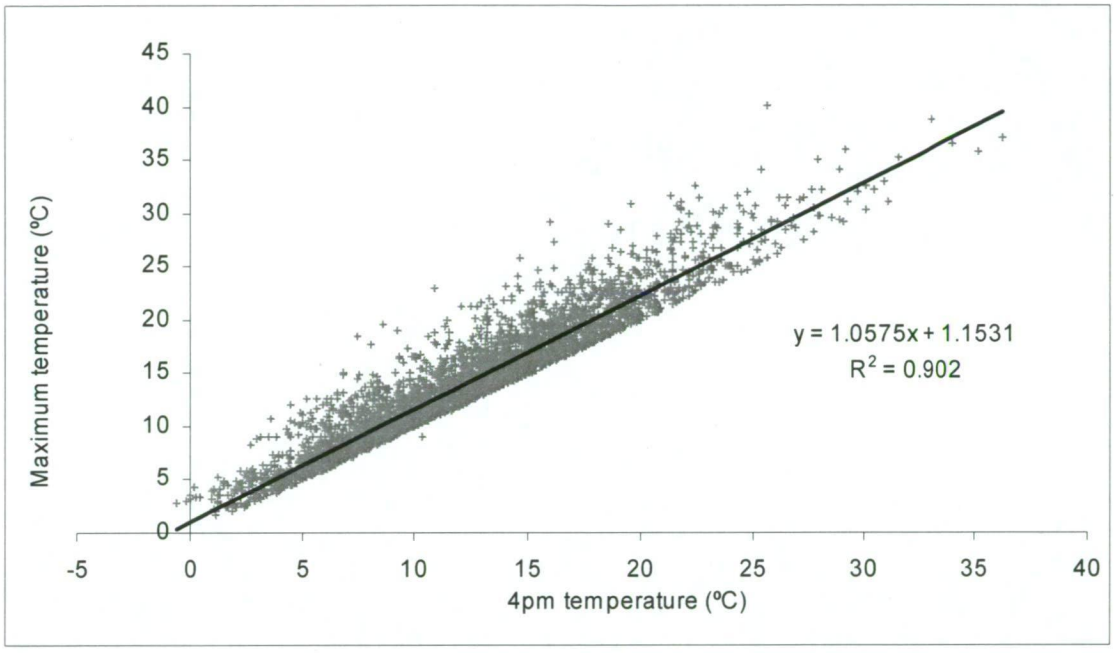

Figure 2.8. Correlation between maximum daily temperatures and 4 pm daily temperatures in 14 sites unaffected by direct sunlight. The regression equation may be used to estimate maximum temperature from 4 pm temperature.

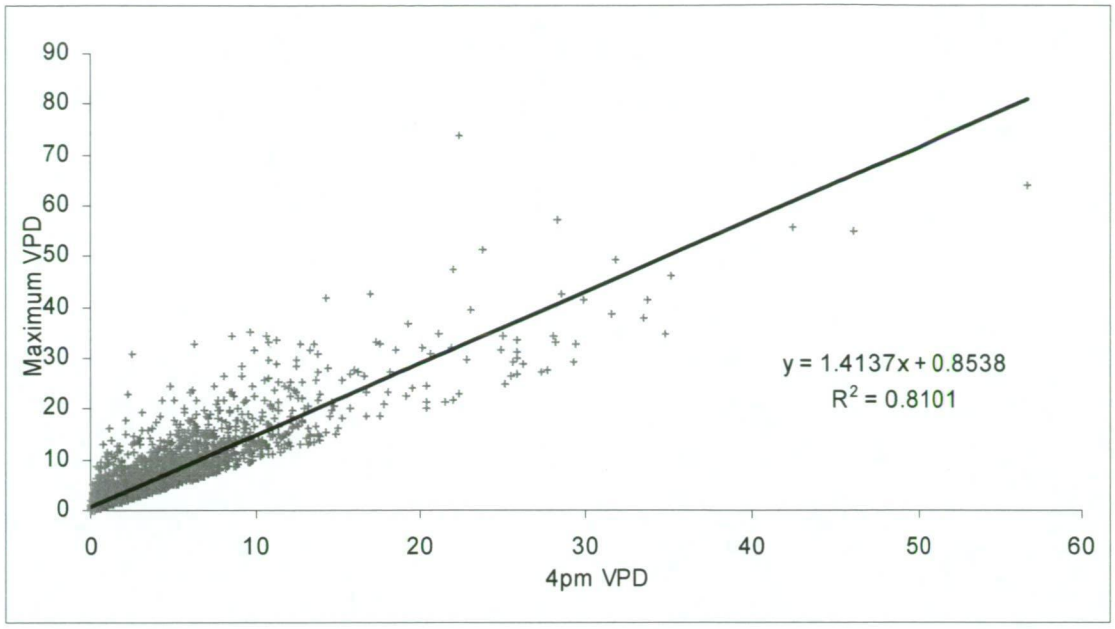

Figure 2.9. Correlation between maximum daily vapour pressure deficit and 4 pm daily vapour pressure deficit in 14 sites unaffected by direct sunlight. The regression equation may be used to estimate maximum vapour pressure deficit from 4 pm vapour pressure deficit.

2.3.4 Analysis of all data

Restricted maximum likelihood (REML) analysis of variance was performed with JMP7 (SAS 2007). The data for each analysis was checked for normality and homoscedacity assumptions, and transformed as necessary. Post Hoc tests used least squares means Tukey's test which is conservative for different sample sizes (Tukey 1991). All analyses were performed on individual log data except where such data was not available (e.g. for mesoclimatic measurements, for which only one logger was placed in each site).

2.3.5 Analysis of species richness for each log

Species richness data for all species and the taxonomic groups moss, liverwort and fern species were generated by converting the Braun-Blanquet cover abundance scores to simple presence or absence for each log. Per-log species richness of all species, mosses only, liverworts only and ferns only were calculated from this data. This was analysed for regenerating forest age effect with REML anova, with log diameter as a covariate to account for the differences that log diameter may have on relative species richness. The analyses were based on the following model: Number of species = age + site(age) + residual + log diameter where age and log diameter are fixed effects and site(age) is the

random effect of site within age. The latter effect was used as the error term for testing the effect of regenerating forest age. Decay-class effect was analysed with REML anova, with log diameter as a covariate of the model: Number of species = site(decay class) + decay-class + log diameter, where site (decay-class) is a random effect of site within decay-class and decay-class is a fixed effect.

2.3.6 Analysis of species percentage cover for each log

For REML analyses of cover variables per-log percentage cover was calculated for each species as follows. Braun-Blanquet scores for each log were converted to the median value for the range of each score (1 = rare, contributes minimally to cover and was replaced with a zero value; 2 = < 1% and was replaced with a value of 0.5; 3 = 1 - 5%, replaced with 3; 4 = 6 - 25%, replaced with 15; 5 = 26 - 50%, replaced with 37.5; 6 = 51 - 75%, replaced with 62.5; 7 = 76 - 100%, replaced with 87.5). Total covers for all species, mosses only, liverworts only and ferns only were then calculated by summing the score for the relevant species.

The per log percentage covers were analysed with REML analysis of the following model: cover = age + site(age) + residual where age was a fixed effect and site(age) was the random effect of site within regenerating forest age. The latter effect was used as the error term for testing the effect of regenerating forest age. Decay-class effects were analysed with REML analysis of the model: cover = site(decay-class) + decay-class where site(decay-class) was a random effect of site within decay-class and decay-class is a fixed effect.

2.3.7 Analysis of temperature, vapour pressure deficit and log moisture

The average daily 4pm maximum, minimum temperatures, maximum 4 pm vapour pressure deficit and minimum vapour pressure deficit were analysed with REML of the following model: Temperature = age + miniseason + age*miniseason where age and miniseason were fixed effects and age*miniseason was the random effect. Log moisture data were means of six readings for each log per site (three per log for each of the two days. The readings differed between days only for the 8 year old forest ($P < 0.05$). The average log moistures were analysed with REML of the following model: Log moisture = age + site(age) + residual where age is a fixed effect and site(age) was the random effect of site within regenerating forest age. Decay-class effect was analysed with REML of the model:

Log moisture = decay-class + site + site*decay where site*decay-class + residual is a random effect and decay-class and site are fixed effects.

2.3.8 Tests of differences in community composition

Ordination was used to create a visual representation of the variation in community structure using percent cover data for each of the three datasets: The primary dataset, and the two secondary datasets. MDS ordinations were performed with the software PRIMERv6 using Bray-Curtis similarity (Clarke and Gorley 2006). This is a standard measure of similarity used in analysis of ecological community data (Crawley 1997). Two and three dimensional analyses were generated. Because the stress results of each were acceptable, only the two dimensional ordination plots were presented in this thesis.

The software PERMANOVA (Anderson 2005) was used to determine significant differences in per-log community composition based on a subset of data from the secondary dataset that includes only decay class 3 logs in two regenerating forest ages (32 and 43). This subset allowed for a balanced design for determining the difference between regenerating forest ages 32 and 43 only on logs of decay class 3. This software performs multivariate analysis of variance based on a similarity matrix, and is based on statistically robust permutation tests. A Bray-Curtis similarity of Braun-Blanquet scores of species abundance was used, with scores for each species standardised so that they range from zero to one, to give all species equal weighting. The analyses followed the model: Community composition = forest age + site + forest age*site + site(forest age) + residual

Constrained ordinations were performed using CAP (Anderson 2004), to provide an indication of how strongly the constraint of age or decay class represents any realistic differentiation in the two factors on community data. Two dimensional analyses of the primary data set were used for regenerating forest age and decay effects separately and the strongest axes from each based on the percentage of variation explained were used to generate a constrained ordination plot with one axis representing the major variation in response to decay class and the other the major response to regenerating forest age.

Species indicator analysis was used to determine if any individual species had significant age class associations based on percentage cover of species using PC-ORD (McCune and Mefford 1999). The primary dataset was used and species relationships with both regenerating forest age and decay class were examined using a Monte Carlo test of significance of observed maximum indicator value for each species.

Pearsons χ^2 tests were used to determine if there was any significant deviation from predicted frequency of individual species according to age using presence/absence data of the primary dataset including all regenerating forest ages and decay classes. This was done for all species that occurred on more than 9% of logs. Similar analyses was also performed for each secondary dataset to test for differences with decay class within the 20 year old sites and for differences with age on decay class 3 logs.

3. RESULTS

3.1 The succession of cryptogam communities on coarse woody debris after clearfell, burn and sow harvesting

3.1.1 The bryophyte and fern flora on logs

A total of 63 bryophyte (29 mosses and 34 liverworts) and 11 fern species were recorded on 220 logs. The most common species were three mosses (*Wijkia extenuata*, *Rhizogonium novae-hollandiae* and *Dicranoloma billarderi*) and three liverworts (*Telaranea tridactylis*, *Cephaloziella exiliflora* and *Riccardia crassa*), each of which was recorded on at least 30% of logs sampled (Table 3.1). Other common species occurring on more than 15% of logs included the mosses *Dicranoloma robustum*, *Campylopus introflexus*, *Rhizogonium distichum* and *Ptychomnion aciculare* and the liverworts *Riccardia crassa*, *Cephaloziella hirta*, *Riccardia cochleata*, *Bazzania adnexa*, *Lepidozia ulothrix*, *Chiloscyphus semiteres* and *Zoopsis argentea*. A species list arranged into families is provided in Appendix 1.

3.2 Community trends and regenerating forest age based on the primary dataset including all sites and decay classes

Average species richness of all species for each log and average percentage cover of all species for each log increased with time since regeneration burn. The 43 year old regenerating forest had significantly higher average species richness per log than the 8 and 20 year old forest but not the 32 year forest (Figure 3.1). Although the covariate log diameter had a strong, positive association with species richness, the removal of this co-variance had no effect on the significance levels of the comparisons among forest ages. Average per log percentage cover was significantly higher in the 43 year old regenerating forests ($P < 0.001$) than the 8, 20 and 32 year old regenerating forests (Figure 3.2).

Ordination of community data showed a distinct separation between the 43 and 8 year old regenerating forests along axis 2 (Figure 3.3). The 20 and 32 year old regenerating forests were very similar in their distribution within the ordination and this area had a large overlap with both the 8 and 43 year old regenerating forest ages with only 8 points out of a total of 220 outside the 20 and 32 year old regenerating forests' distribution.

Table 3.1. Bryophyte species identified and their frequency of occurrence on total logs sampled (220) expressed as a percentage. *species chosen for detailed analysis.

MOSSES	%	LIVERWORTS	%	FERNS	%
*Wijkia extenuata**	45.0	*Telaranea tridactylis**	39.1	*Histiopteris incisa*	7.3
*Rhizogonium novae-hollandiae**	44.1	*Cephaloziella exiliflora**	33.2	*Hymenophyllum flabellatum*	5.0
*Dicranoloma billarderi**	36.8	*Riccardia crassa**	30.9	*Dicksonia antarctica*	5.0
*Dicranoloma robustum**	25.9	*Cephaloziella hirta**	21.8	*Hymenophyllum cupressiforme*	4.1
*Campylopus introflexus**	23.2	*Riccardia cochleata**	21.4	*Rumohra adiantiformis*	3.6
*Rhizogonium distichum**	17.3	*Bazzania adnexa**	20.5	*Grammitis billardierei*	3.2
*Ptychomnion aciculare**	16.8	*Lepidozia ulothrix**	19.5	*Blechnum wattsii*	2.7
*Achrophyllum dentatum**	9.1	*Zoopsis argentea**	16.8	*Polystichum proliferum*	2.3
Leptotheca gaudichaudii	8.6	*Chiloscyphus semiteres**	16.8	*Pteridium esculentum*	1.4
Dicranoloma dicarpum	7.3	*Lepidozia laevifolia*	6.4	*Hymenophyllum rarum*	1.4
Rhaphidorrhynchium amoenum	6.9	*Heteroscyphus coalitus*	6.4	*Hypolepis rugosula*	0.5
Hypnum chrysogaster	5.5	*Gackstroemia weindorferi*	4.5		
Leucobryum candidum	3.6	*Heteroscyphus fissistipus*	3.2		
Thuidiopsis sparsa	3.6	*Schistochila lehmanniana*	2.7		
Moss sp 1	3.2	*Riccardia aequicellularis*	2.3		
Distichophyllum pulchellum	2.3	*Chiloscyphus multipennus*	2.3		
Orthodontium lineare	1.8	*Chiloscyphus latifolius*	2.3		
Rosulabryum billarderi	1.8	*Podomitrium phyllanthus*	1.8		
Goniobryum subbasilare	1.4	*Hymenophyton flabellatum*	1.8		
Rhynchostegium tenuifolium	1.4	*Liverwort sp a*	1.4		
Cyathophorum bulbosum	0.5	*Lepidozia glaucophylla*	1.4		
Dicranoloma menziesii	0.5	*Jamesoniella tasmanica*	1.4		
Hypnodendron comosum	0.5	*Acromastigum colensoanum*	1.4		
Hypopterygium didictyon	0.5	*Kurzia compacta*	0.9		
Leptostomum inclinans	0.5	*Cuspidatula monodon*	0.9		
Pohlia nutans	0.5	*Cyanolophocolea echinella*	0.9		
Polytrichum juniperinum	0.5	*Heteroscyphus biciliatus*	0.9		
Racopilum cuspidigerum	0.5	*Zoopsis setulosa*	0.5		
Tayloria gunnii	0.5	*Tylimanthus pseudosaccatus*	0.5		
		Tylimanthus diversifolius	0.5		
		Telaranea herzogii	0.5		
		Metzgeria furcata	0.5		
		Chiloscyphus muricatus	0.5		
		Acromastigum mooreanum	0.5		

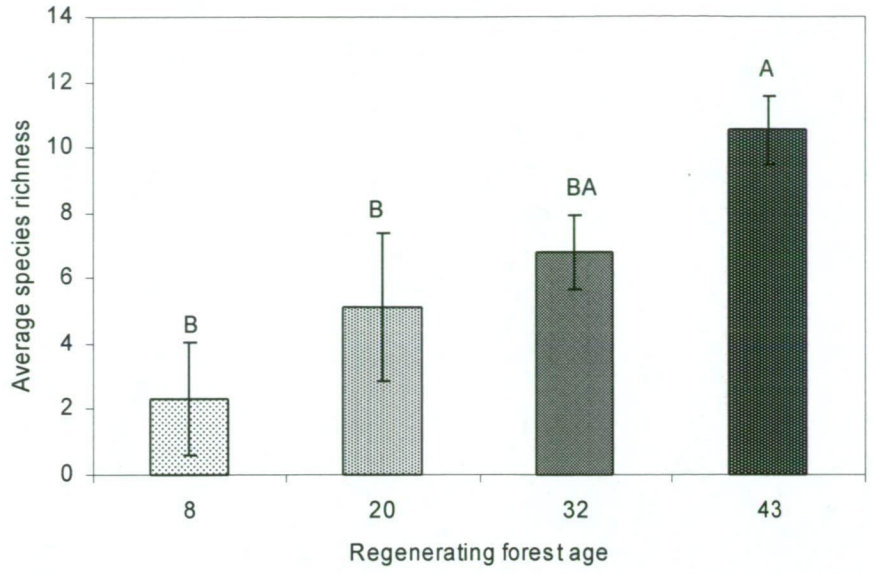

Figure 3.1. Average epixylic species richness on logs (± standard error) of all species for each regenerating forest age. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed highly significant differences among means between forest ages ($P < 0.01$). The covariate log diameter had a significant effect ($P < 0.01$). Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different from each other ($P > 0.05$).

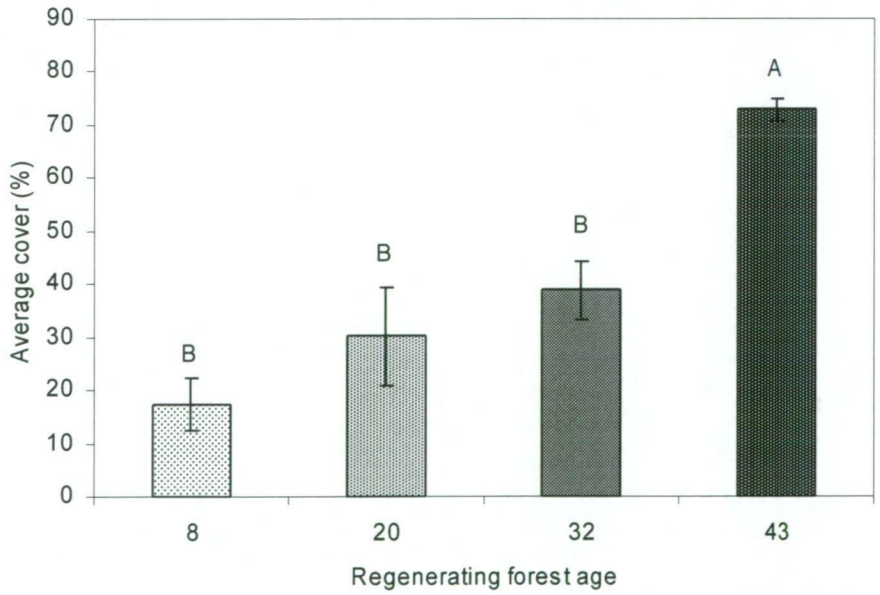

Figure 3.2. Average epixylic species cover on logs (% ± standard error) of all species for each regenerating forest age. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed very highly significant differences among means ($P < 0.001$). Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

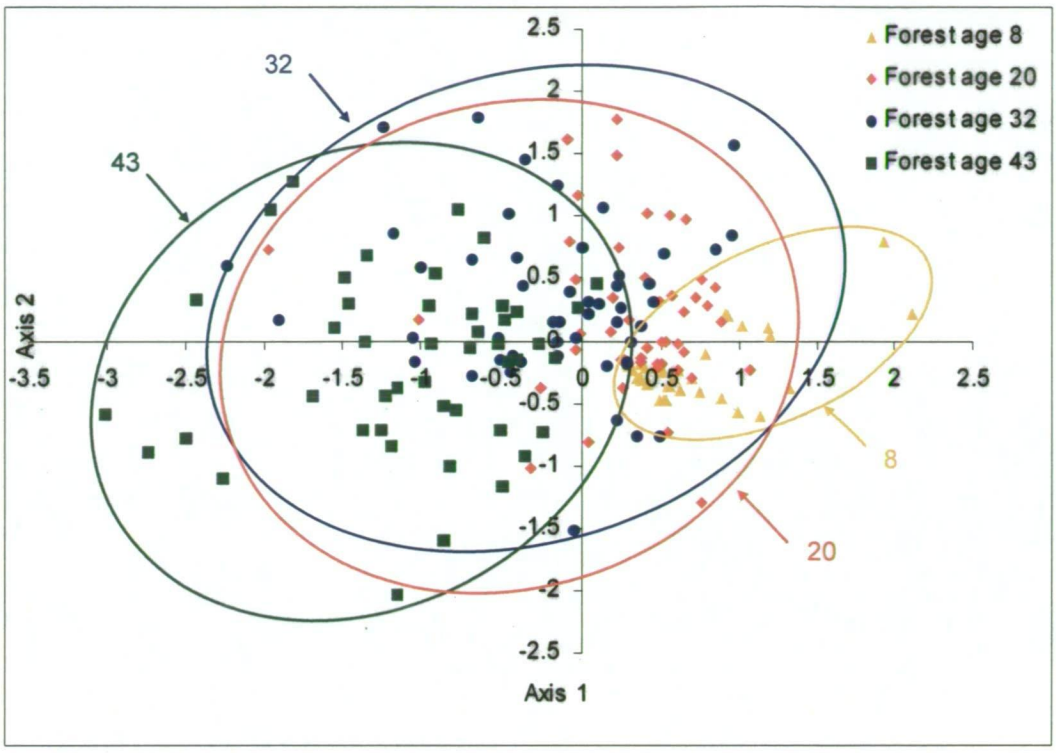

Figure 3.3. Ordination plot of percentage cover of all epixylic species on each log showing regenerating forest age groupings, based on MDS in two dimensions (Stress = 0.19). Values are from the primary dataset including all regenerating forest ages and decay classes.

The patterns of community change with regenerating forest age varied among taxonomic groups. Species richness of mosses, liverworts and ferns all tended to increase with forest age (Figure 3.4), with the moss and liverwort groups showing significant differences between the youngest regenerating forest and the oldest regenerating forest ages. Although the covariate log diameter had a positive association with the mosses, it had no effect on the significance levels of the comparisons among ages. The covariate log diameter had no significant effect on the species richness of liverworts or ferns. Ferns had higher species richness in the 43 year old forest than the 8 year old forest, though this was not statistically significant, and smaller changes in species richness in the other forest ages.

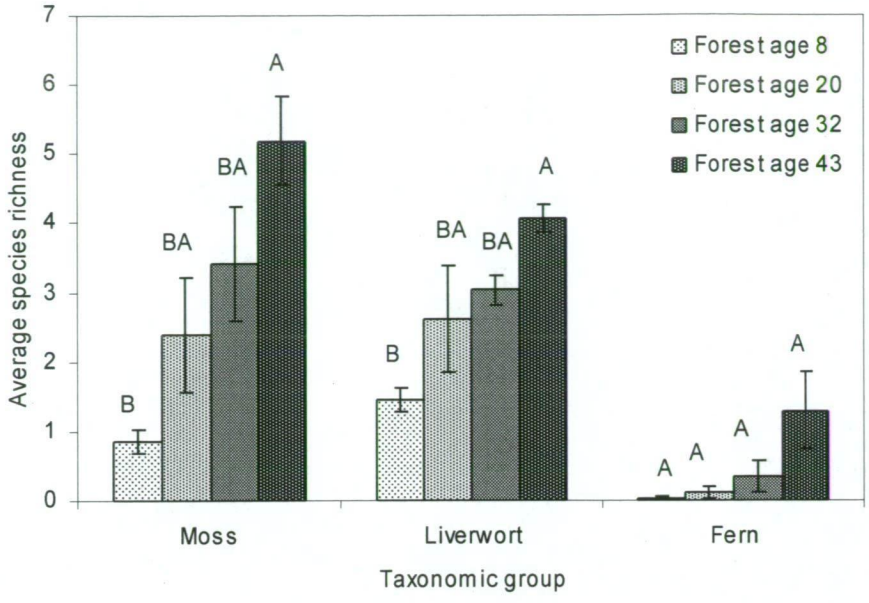

Figure 3.4. Average epixylic species richness on logs (± standard error) of taxonomic groups for each regenerating forest age. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed highly significant differences among means for forest ages for mosses ($P < 0.01$), liverworts ($P < 0.01$) but not the ferns. The covariate log diameter had a significant effect for mosses ($P < 0.01$) but not the liverwort or ferns. Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

Moss, liverwort and fern percentage cover per log showed broadly similar patterns to those shown in species richness. Mosses increased consistently in abundance over time, with 43 year old forests having significantly more percentage cover than 8 and 20 year old forests, and 32 year old forests having significantly more percentage cover than 8 year old forests ($P < 0.01$; Figure 3.5). Liverworts were not significantly different between the 8, 20 and 32 year old forests but had a much higher average percentage cover per log in the 43 year old forest. Ferns had higher (but not significantly higher) abundance in the 43 year old forest.

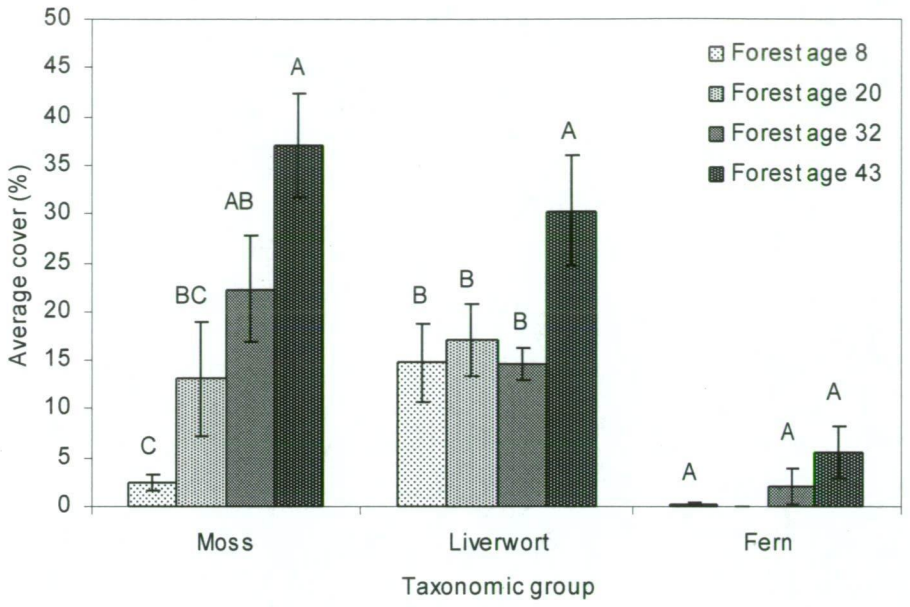

Figure 3.5. Average cover on logs (% ± standard error) of taxonomic groups for each regenerating forest age. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed very highly significant differences among means for mosses ($P < 0.01$) and liverworts ($P < 0.05$) but not for ferns. Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

3.3 Community trends with decay class

In the primary data set (including all regenerating ages and decay classes) average species richness of all species for each log was greatest on decay classes 3 and 4 (means of 8.1 and 7.3; respectively), and lowest on decay class 2 (2.5 species per log), with decay class 5 intermediate (Figure 3.6). Although the covariate log diameter had a similar relationship with species richness, removing the effect of the covariate had no effect on the significance levels of the comparisons between decay classes. Average percentage cover showed similar patterns (Figure 3.7).

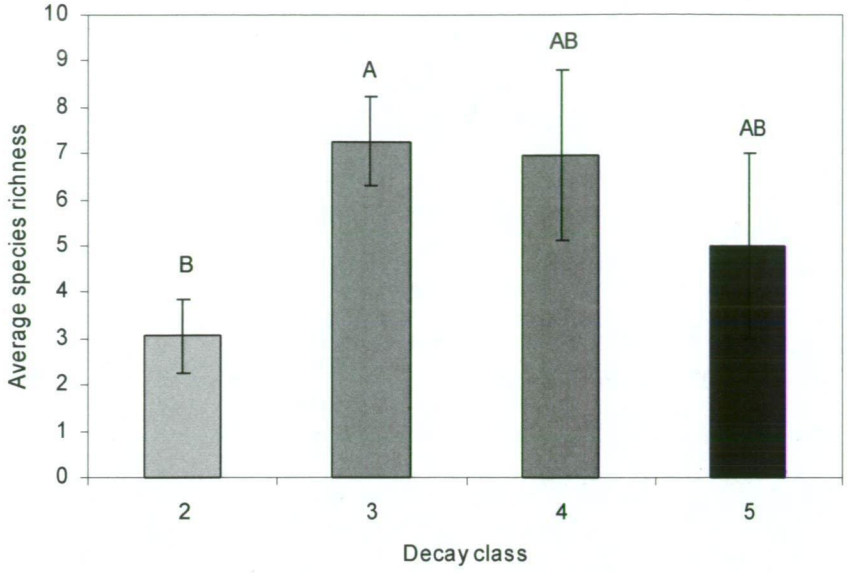

Figure 3.6. Average epixylic species richness on logs (± standard error) of all species for each decay class. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed significant differences among means ($P < 0.05$). The covariate log diameter had a significant effect ($P < 0.01$). Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

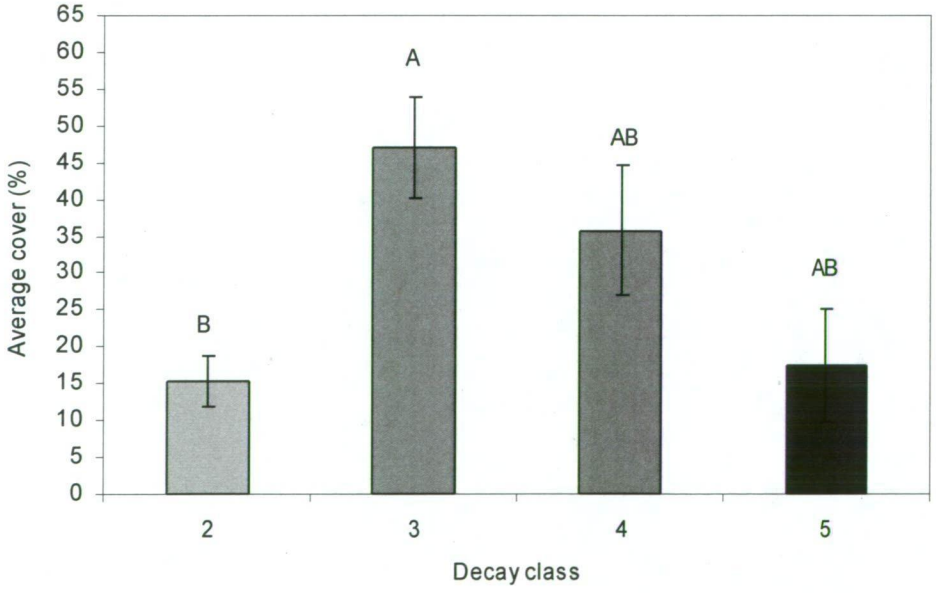

Figure 3.7. Average cover on logs (% ± standard error) of all species for each decay class. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed no significant differences among means ($P > 0.05$). Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P < 0.01$).

Ordination of percentage cover on each log of community data grouped by decay class indicated very little separation between decay classes (Figure 3.8). Decay class 3 and 4 were relatively widely scattered in the plot when compared decay class 2. All decay classes showed a tendency to group closer towards the centre of the plot, along with decay class 5.

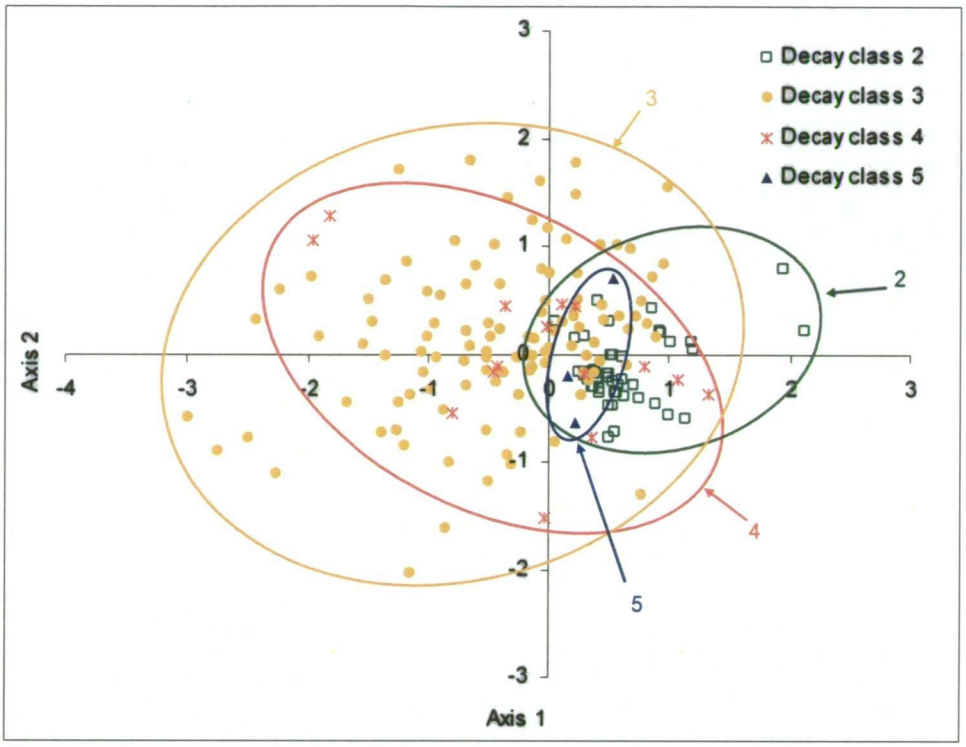

Figure 3.8. Ordination plot of percentage cover of all epixylic species on each log showing decay class groupings, based on MDS in two dimensions (Stress = 0.19). Values are from the primary dataset including all regenerating forest ages and decay classes.

3.4 Individual species associations with regenerating forest age and decay

The analyses here used three different measures of species specific association with forest age - REML analysis of variance of percentage cover on logs; indicator species analysis implemented in CAP and χ^2 tests of the total frequency of occurrence for each regenerating forest age (Table 3.2). These measures all showed that the species vary greatly in their associations with different forest ages. All three measures showed that the liverwort *Chiloscyphus semiteres* was not significantly associated with any forest age and therefore can be interpreted as a generalist species. All three measures showed that the liverworts *Cephaloziella hirta* and *Cephaloziella exiliflora* and the moss *Campylopus introflexus* were strongly associated with younger regenerating forests, and therefore can be interpreted as

early successional species. All three measures showed that the liverwort *Riccardia crassa* was strongly associated with the 20 year old forest and that in two out of three measures the moss *Dicranoloma robustum* and the liverwort *Riccardia cochleata* were significantly associated with the 32 year old forest, and therefore these species can be interpreted as mid-successional. Two out of the three measures showed that the liverwort *Lepidozia ulothrix* and the mosses *Achrophyllum dentatum*, *Ptychomnion aciculare* and *Dicranoloma billarderi* were all significantly associated with the 43 year old forest. Similarly, significantly associated with the 43 year old forest were the liverworts *Zoopsis argentea*, *Bazzania adnexa*, *Telaranea tridactylis*, and the mosses *Rhizogonium distichum*, *Wijkia extenuata* and *Rhizogonium novae-hollandiae* in all three measures. Therefore these species significantly associated with the 43 year old forests can be interpreted as late successional species.

Table 3.2. Associations of individual species with regenerating forest age based on analysis of the primary dataset, which includes all regenerating forest ages and decay classes. Species chosen occurred on more than 9% of the 220 logs sampled. Taxonomic group shows if a species is either a moss or liverwort, % shows the percentage of logs out of 220 that each species occurred on, REML (*P*) is the analysis of variance for percentage cover per log. Indicator species analysis describes the forest age that each species was significantly associated with, the indicator value (IV) for each species and the significance value (*P*). Pearson's χ^2 test significance values (*P*) are given for species presence (frequency). Values in bold are significant.

			REML (*P*)	Indicator species analysis			χ^2 tests (*P*)
Species	Taxonomic group	%	% cover	Forest age	IV	*P*	Frequency
Chiloscyphus semiteres	Liverwort	16.8	0.6790	32	7.4	0.442	0.0667
Cephaloziella hirta	Liverwort	21.8	**0.0277**	8	55.1	**0.001**	**<0.0001**
Cephaloziella exiliflora	Liverwort	33.2	**0.0263**	8	30.8	**0.001**	**<0.0001**
Campylopus introflexus	Moss	23.2	**0.0030**	8	36.4	**0.001**	**<0.0001**
Riccardia crassa	Liverwort	30.9	**0.0162**	20	26	**0.001**	**<0.0001**
Dicranoloma robustum	Moss	25.9	0.4044	32	17.8	**0.004**	**0.0002**
Riccardia cochleata	Liverwort	21.4	0.0662	32	29.5	**0.001**	**<0.0001**
Lepidozia ulothrix	Liverwort	19.5	0.3801	43	15.6	**0.005**	**0.0004**
Zoopsis argentea	Liverwort	16.8	**0.0038**	43	29.3	**0.001**	**<0.0001**
Achrophyllum dentatum	Moss	9.1	0.2956	43	22.1	**0.001**	**<0.0001**
Ptychomnion aciculare	Moss	16.8	0.0736	43	20.6	**0.001**	**0.0016**
Rhizogonium distichum	Moss	17.3	**0.0479**	43	36.7	**0.001**	**<0.0001**
Bazzania adnexa	Liverwort	20.5	**0.0006**	43	58.9	**0.001**	**<0.0001**
Dicranoloma billarderi	Moss	36.8	0.0877	43	27.9	**0.001**	**<0.0001**
Wijkia extenuata	Moss	45	**0.0037**	43	50.2	**0.001**	**<0.0001**
Rhizogonium novae-hollandiae	Moss	44.1	**<0.0001**	43	50.7	**0.001**	**<0.0001**
Telaranea tridactylis	Liverwort	39.1	**<0.0001**	43	59.6	**0.001**	**<0.0001**

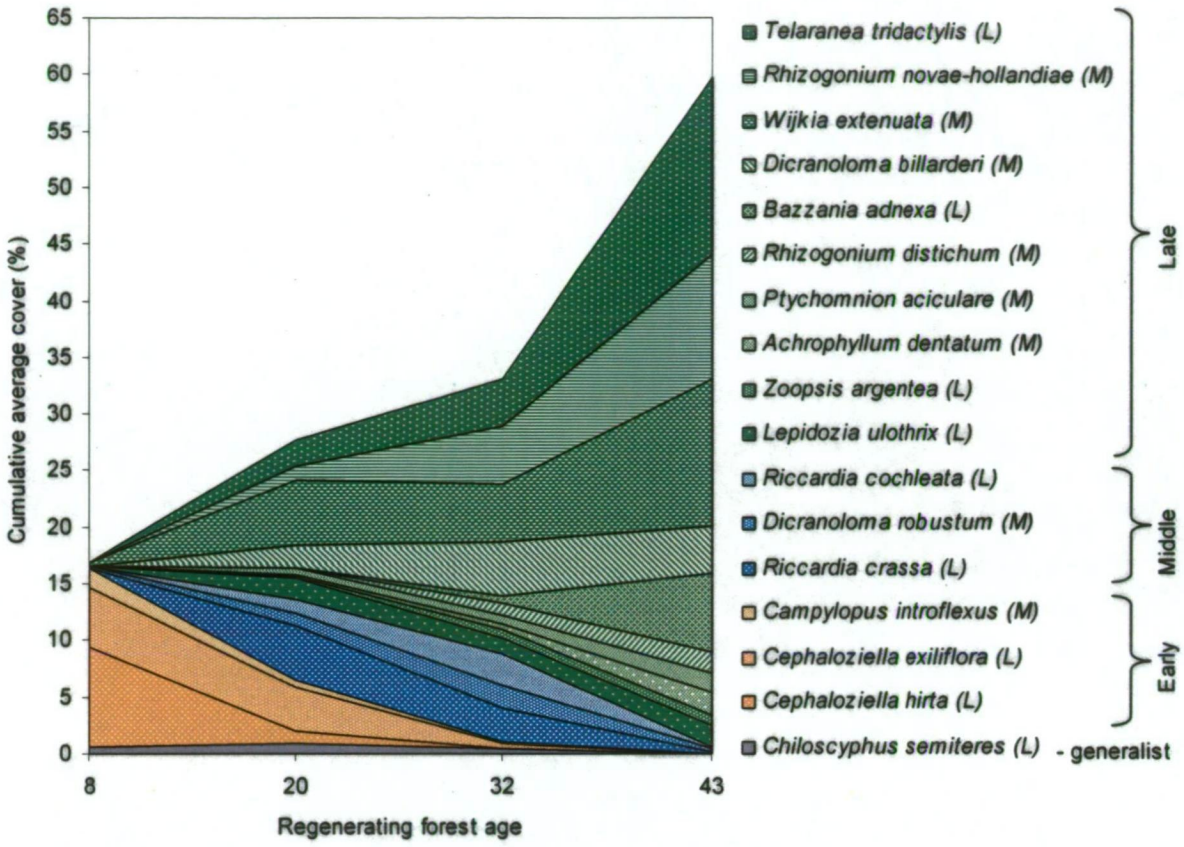

Figure 3.9. Average cover (%) on logs for each species occurring on at least 9% of logs using the primary dataset including all regenerating forest ages and all decay classes. Species are colour coded according to inferred successional characteristics. Abbreviations: M = moss, L = Liverwort.

3.5 Segregating the effects of regenerating forest age and log decay

3.5.1 The independent effects of regenerating forest age on coarse woody debris cryptogam community succession.

Average epixylic species richness on logs for all species and percentage cover, based on the secondary dataset including the three regenerating forest ages 20, 32 and 43 on logs of decay class 3, tended to increase with forest age, although these differences were not significant (Figures 3.10 and 3.11). The covariate log diameter had a positive relationship with species richness. However, it had no effect on the significance levels of the comparisons among ages. Average percentage cover for each log was significantly greater in the 43 year old forest than both the 20 and 32 year old forests ($P < 0.01$).

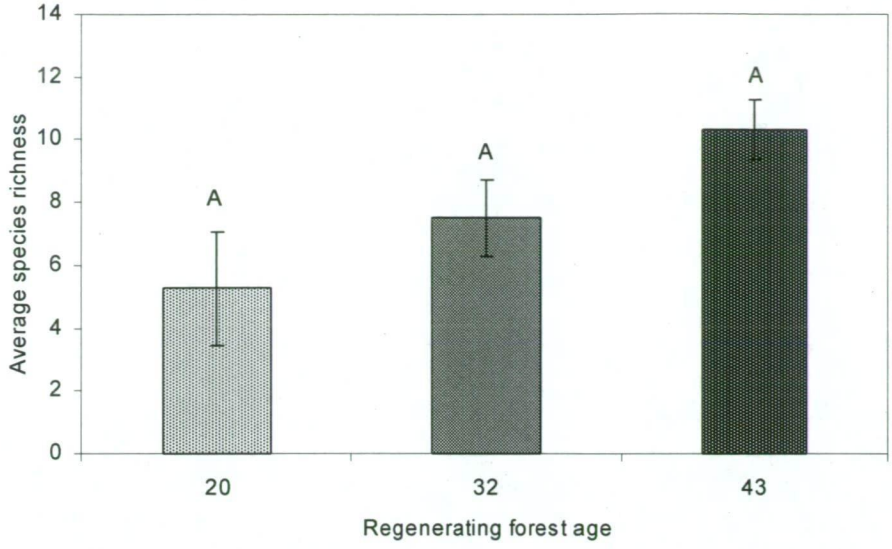

Figure 3.10. Average epixylic species richness on logs (± standard error) of all species for each regenerating forest age. Values are from the secondary dataset including the regenerating forest ages 20, 32 and 43 on logs only of decay class 3. Analysis of variance showed no significant differences among means ($P > 0.05$). The covariate log diameter had a significant effect ($P < 0.01$). Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

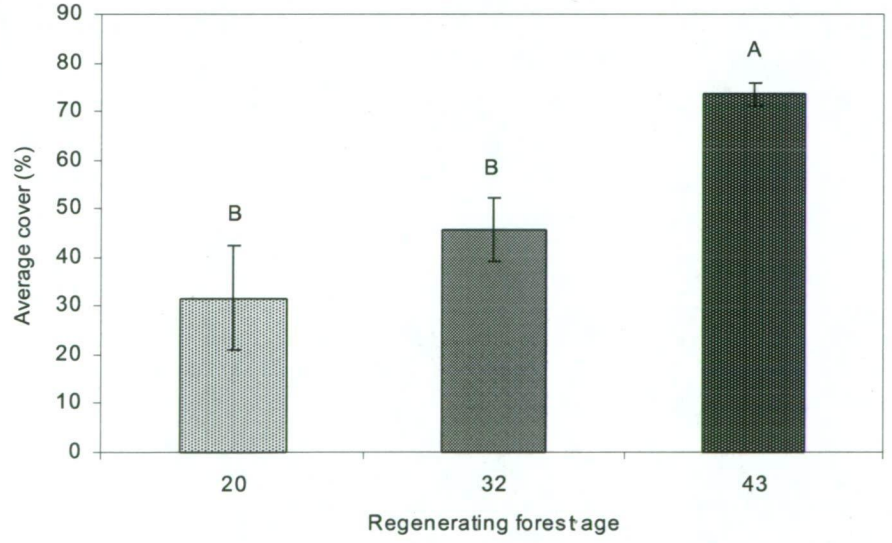

Figure 3.11. Average cover on logs (% ± standard error) of all species for each regenerating forest age. Values are from the secondary dataset including the three regenerating forest ages 20, 32 and 43 on logs of decay class 3. Analysis of variance showed significant differences among means ($P < 0.01$). Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

The taxonomic groups mosses, liverworts and ferns showed similar trends in this restricted data set to those shown by all species, where there appeared to be a small increase in average species richness per-log with increasing forest age (Figure 3.12). However no taxonomic group showed significant differences between regenerating forest ages when tested using REML ($P > 0.05$). The covariate log diameter was positively associated with species richness. However, it had no effect on significance levels among forest ages. Average percentage cover per log was not significantly different for mosses or ferns ($P > 0.05$) however there was a significantly ($P < 0.05$) higher cover of liverworts in the 43 year old forest than the 32 year old forest (Figure 3.13).

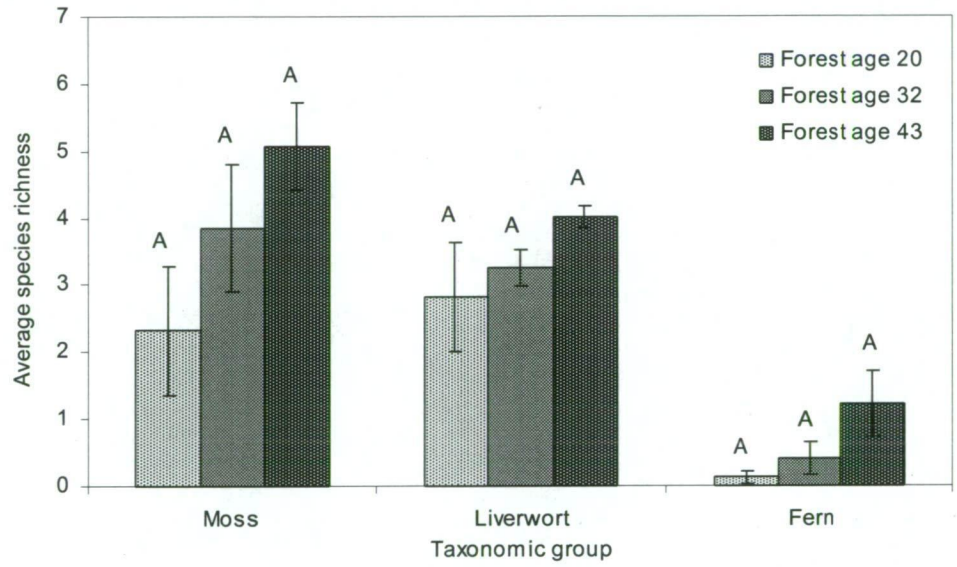

Figure 3.12. Average epixylic species richness on logs (± standard error) of taxonomic groups for each regenerating forest age. Values are from the secondary dataset including the three forest ages 20, 32 and 43 on logs of decay class 3. Analysis of variance showed no significant differences among means for any group ($P > 0.05$). The covariate log diameter had a significant effect for mosses ($P < 0.05$) and ferns ($P < 0.05$) but not for liverworts. Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

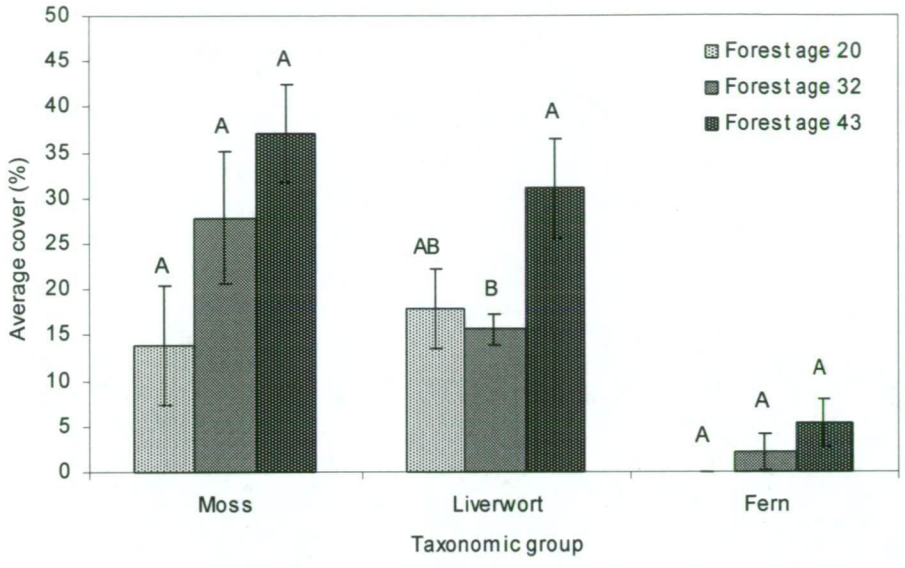

Figure 3.13. Average cover on logs (% ± standard error) of taxonomic groups for each regenerating forest age. Values are from the secondary dataset including the three regenerating forest ages 20, 32 and 43 on logs of decay class 3. Analysis of variance showed significant differences among means for Liverworts ($P < 0.05$) but not mosses or ferns. Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

Ordination of percentage cover of all species for each log showed a very strong grouping for the 43 year regenerating forest (Figure 3.14). The 32 year old forest also had a strong grouping and the 20 year old forest was less tightly grouped, with each successive regenerating forest age showing a tendency for closer groupings as values increased across axis 2 of the ordination. PERMANOVA analysis of community data on decay class 3 logs found significant differences ($P < 0.05$) between the 32 and 43 year old forests.

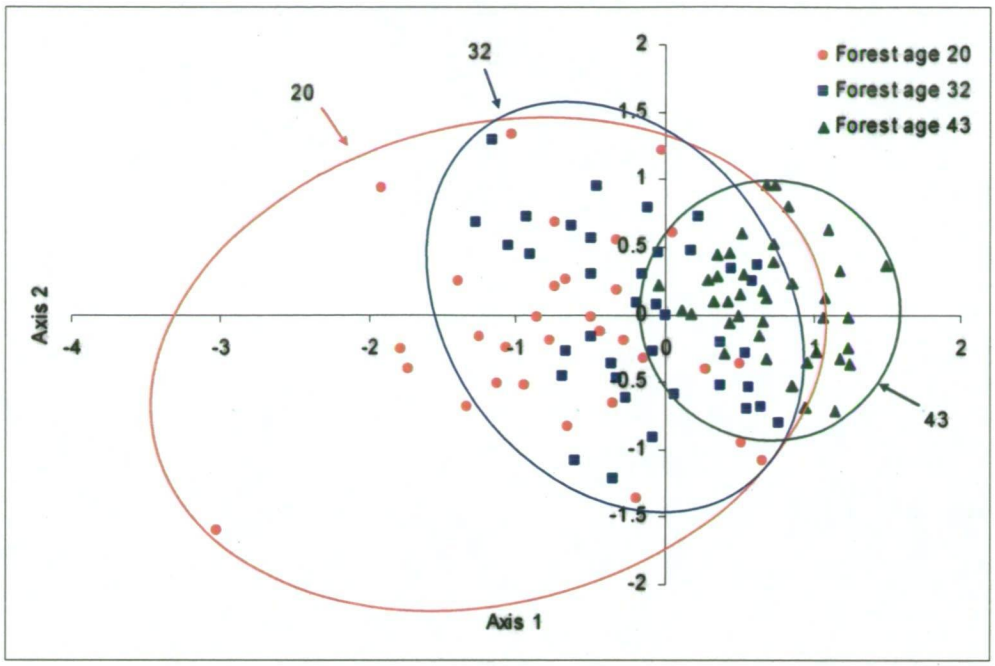

Figure 3.14. Ordination plot of percentage cover for each log for all species showing regenerating forest age groupings, based on MDS in two dimensions (Stress = 0.23). Values are from the secondary dataset of regenerating forest age independent of decay class.

Two of the measures of species specific association with forest age could be used with this restricted data - REML analysis of variance of percentage cover on logs and χ^2 tests of the total frequency of occurrence for each of the three regenerating forest ages (Table 3.3). These measures showed that the species varied greatly in their associations with different forest ages independent of decay class. In addition to the liverwort *Chiloscyphus semiteres* (which had been identified as a generalist from the primary dataset including all ages and decay classes), both measures implied that the liverwort *Lepidozia ulothrix* and the mosses *Campylopus introflexus*, *Dicranoloma robustum* and *Dicranoloma billarderi* were successional generalists. Early successional species were not revealed in this analysis as the 8 year old forest did not have any logs of decay class 3 and was excluded. Similar to the analysis of age effects from the primary dataset including all forest ages and decay classes, the liverworts *Riccardia crassa* and *Riccardia cochleata* both had significant associations with either the 20 or 32 year old forests and can be interpreted as mid-successional; however, for *Riccardia cochleata* this was only significant for frequency of occurrence. The liverwort *Cephaloziella exiliflora* may be considered mid-successional based on significance in both measures for the 20 or 32 year old forests. The liverwort *Cephaloziella hirta* also may be interpreted as mid-successional, however this species had

significant associations with the 20 year old forest based on the measure of frequency of occurrence only. Two liverworts, *Telaranea tridactylis* and *Bazzania adnexa*, and one moss, *Rhizogonium novae-hollandiae*, showed significant associations with the 43 year old forest for both percentage cover and frequency in both this analysis and analysis of age effects based on the primary dataset, including all forest ages and decay classes. The significant association with the 43 year old forest was the same for the mosses *Achrophyllum dentatum* and *Ptychomnion aciculare* in both analysis of frequency of occurrence based on both the primary dataset of all forest ages and decay classes and the secondary dataset of forest age independent of decay class. The mosses *Rhizogonium distichum* and *Wijkia extenuata* were significantly associated with the 43 year old forest for all three measures based on the primary dataset of all forest ages and decay classes; however, based on forest age (independent of decay class) these two species were significantly associated with only the 43 year old forest based on species frequency of occurrence. All species significantly associated with the 43 year old age class in at least one measure can be considered late successional species.

Table 3.3. Individual species associations with regenerating forest age; based on analysis of the secondary dataset of regenerating forest age (independent of decay class) including the three forest ages 20, 32 and 43 on decay class 3 logs. Species chosen occurred on more than 9% of the 220 logs sampled. REML (*P*) is the analysis of variance for % cover for each log per forest age. Pearson's χ^2 test significance values (*P*) are given for species presence (frequency). The forest age column indicates which age class each species was most common in. Values in bold are significant.

		Test of regenerating forest age		
			REML (*P*)	χ^2 tests (*P*)
Species	Taxonomic group	Forest age	% cover	Frequency
Chiloscyphus semiteres	Liverwort	-	0.4477	0.2800
Cephaloziella hirta	Liverwort	20	0.3267	**0.0183**
Cephaloziella exiliflora	Liverwort	20	**0.0006**	**0.0009**
Campylopus introflexus	Moss	-	0.1240	0.2231
Riccardia crassa	Liverwort	20	**0.0206**	**0.0024**
Dicranoloma robustum	Moss	-	0.5822	0.3128
Riccardia cochleata	Liverwort	32	0.0639	**0.0011**
Lepidozia ulothrix	Liverwort	-	0.9942	0.6330
Zoopsis argentea	Liverwort	43	**0.0157**	**0.0010**
Achrophyllum dentatum	Moss	43	0.3619	**0.0015**
Ptychomnion aciculare	Moss	43	0.2895	**0.0433**
Rhizogonium distichum	Moss	43	0.1035	**<0.0001**
Bazzania adnexa	Liverwort	43	**0.0049**	**<0.0001**
Dicranoloma billarderi	Moss	-	0.7644	0.2561
Wijkia extenuata	Moss	43	0.1177	**0.0060**
Rhizogonium novae-hollandiae	Moss	43	**0.0139**	**0.0042**
Telaranea tridactylis	Liverwort	43	0.0016	0.0012

3.5.2 The independent effects of log decay on succession of communities on coarse woody debris.

The analysis of per log data restricted to decay classes 2 and 3 in 20 year old forest showed that there were no significant differences in species richness and average percentage cover of all species between decay classes 2 and 3, both overall and for each taxonomic group (Figure 3.15 - 3.18). Although the covariate log diameter had a positive association with species richness, there was no effect on the significance levels of the comparisons between decay classes when the covariate was removed. Log diameter had no significant association with the species richness of groups between decay classes.

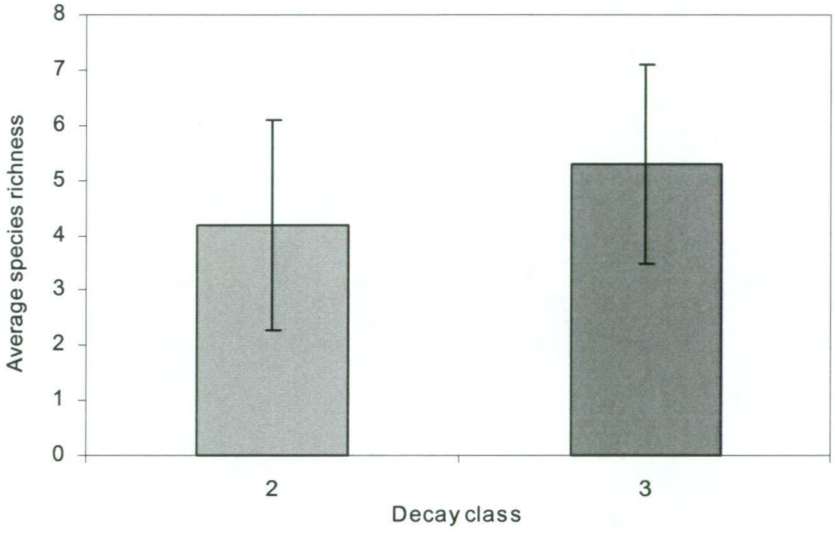

Figure 3.15. Average epixylic species richness on logs (± standard error) of all species for each decay class. Values are from the secondary dataset of decay class (independent of regenerating forest age) including decay classes 2 and 3 in the 20 year old regenerating forest. Analysis of variance showed no significant differences among means ($P > 0.05$). The covariate log diameter had a significant effect ($P < 0.05$).

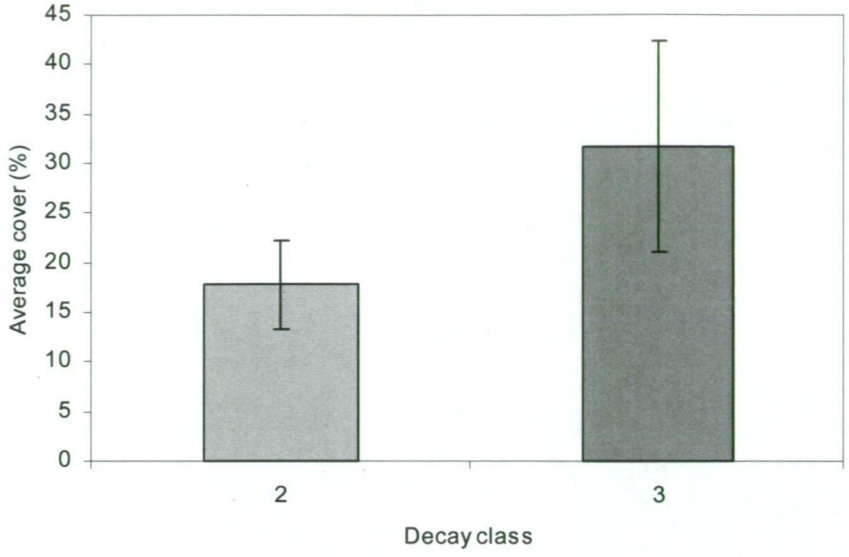

Figure 3.16. Average cover on logs (% ± standard error) of all species for each decay class. Values are from the secondary dataset of decay class (independent of regenerating forest age) including decay classes 2 and 3 in the 20 year old regenerating forest. Analysis of variance showed no significant differences among means ($P > 0.05$).

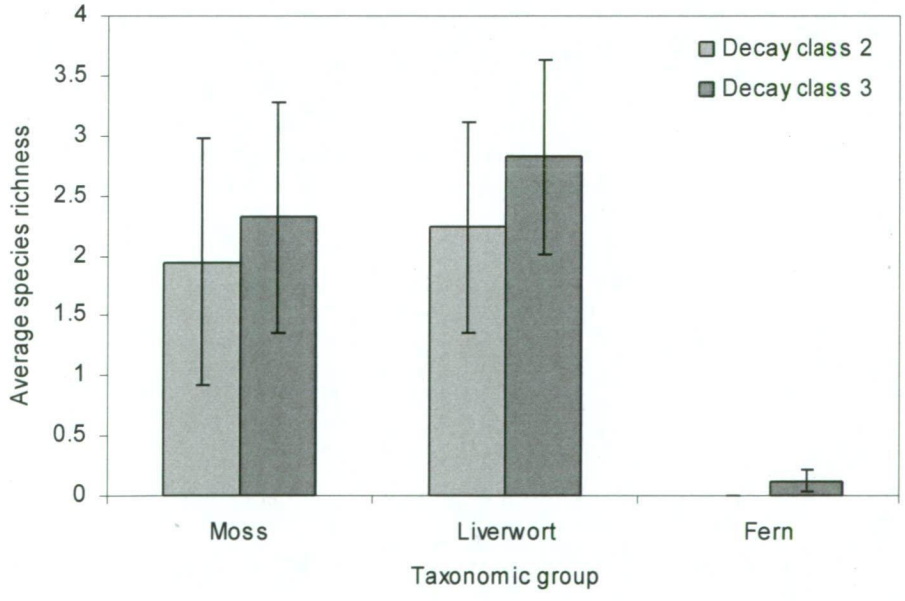

Figure 3.17. Average epixylic species richness on logs (± standard error) of taxonomic groups for each regenerating forest age. Values are from the secondary dataset of decay class independent of regenerating forest age including decay classes 2 and 3 in the 20 year old regenerating forest. Analysis of variance showed no significant differences among means ($P > 0.05$). The covariate log diameter had no significant effect ($P > 0.05$).

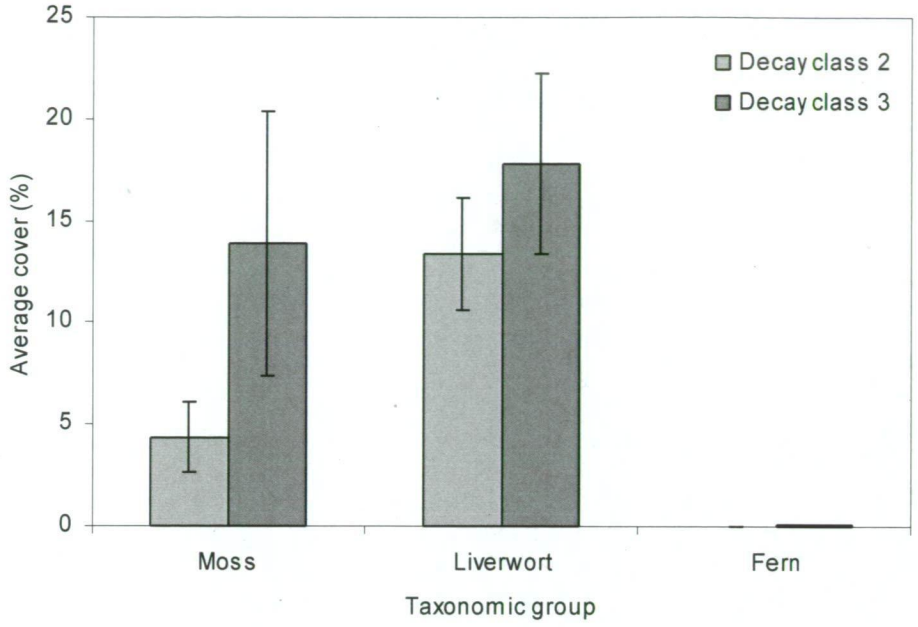

Figure 3.18. Average cover on logs (% ± standard error) of taxonomic groups for each decay class. Values are from the secondary dataset of decay class independent of regenerating forest age including decay classes 2 and 3 in the 20 year old regenerating forest. Analysis of variance showed no significant differences among means ($P > 0.05$).

Unconstrained ordination of per-log community data from the secondary dataset of decay class (independent of regenerating forest age) showed that while there was extensive overlap there was still some discrimination between decay classes (Figure 3.19). Decay class 2 grouped completely with decay class 3 except for 2 points and just over half of decay class 3 grouped outside of decay class 2. The majority of points from each decay class seemed to group independently of the other decay class.

Constrained ordination directly compared the effect of regenerating forest age and decay class on the cryptogam community as a whole using the primary dataset including all regenerating forest ages and decay classes. Overall, it appeared that age was determining more of the grouping than decay class and this was particularly true for the 8, 32 and 43 year regenerating forest ages (Figure 3.20). The spread of the 20 year regenerating forest age was determined mostly by the decay class axis, where the spread along the age axis was small but the spread determined by the decay class axis was broad. Decay class also influenced the 8 year age class, though to a lesser extent with a fairly large spread for both axes.

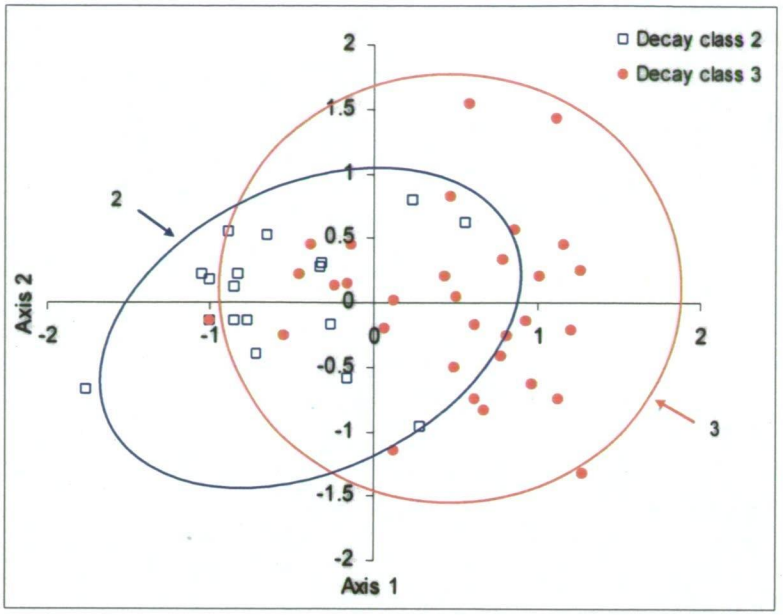

Figure 3.19. Ordination plot of percentage cover on logs of all species showing regenerating forest age groupings, based on MDS in two dimensions (Stress = 0.17). This plot was generated using the secondary dataset of decay class independent of regenerating forest age including decay classes 2 and 3 in only the 20 year old regenerating forest.

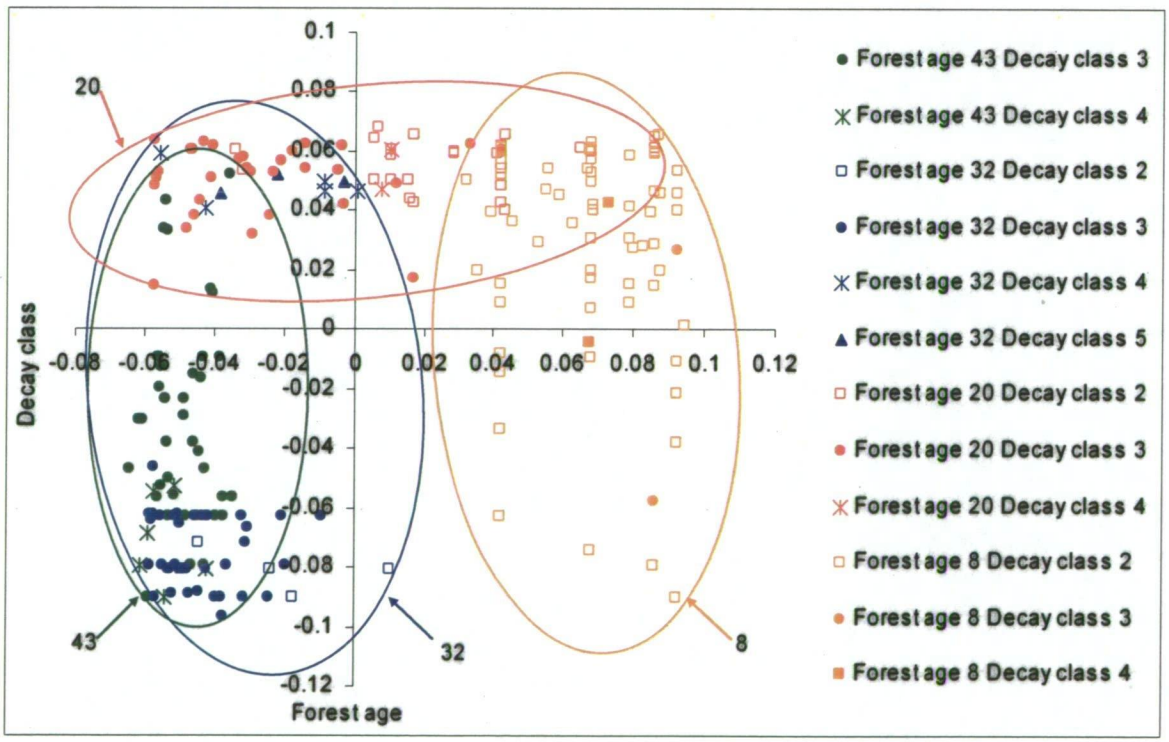

Figure 3.20. Constrained ordination plot of percentage cover on logs. This plot was generated using two analyses of the primary dataset including all floristic data, with one axis representing the forest age constraint and the other axis representing the decay-class constraint.

Individual species analysis of decay class independent of regenerating forest age showed that few species have strong decay class associations based on two measures - REML analysis of variance of percentage cover on logs and χ^2 tests of the total frequency of occurrence for each regenerating forest age (Table 3.4). The liverwort *Riccardia cochleata* and the moss *Telaranea tridactylis* were significantly associated with decay class 3 for both measures. The liverwort *Cephaloziella exiliflora* was significantly associated with decay class 2 based on percentage cover only. The liverworts *Chiloscyphus semiteres*, *Riccardia crassa*, and *Lepidozia ulothrix*, and the mosses *Dicranoloma billarderi* and *Rhizogonium novae-hollandiae* were significantly associated with decay class 3 based on species frequency of occurrence only.

Table 3.4. Individual species associations with decay class based on analysis of the secondary dataset of decay class (independent of regenerating forest age) including decay classes 2 and 3 in the 20 year old forest. Species chosen occurred on more than 9% of the 220 logs sampled. Taxonomic group shows if a species is either a moss or liverwort. REML (*P*) is the analysis of variance for % cover. Pearson's χ^2 test significance values (*P*) are given for frequency of occurrence. Values in bold are significant.

		Test of decay class		
			REML (*P*)	χ^2 tests (*P*)
Species	Taxonomic group	Decay class	% cover	Frequency
Chiloscyphus semiteres	Liverwort	3	0.4800	**0.0196**
Cephaloziella hirta	Liverwort	-	0.6153	0.7054
Cephaloziella exiliflora	Liverwort	2	**0.0257**	0.2353
Campylopus introflexus	Moss	-	0.3598	0.3173
Riccardia crassa	Liverwort	3	0.1149	**<0.0001**
Dicranoloma robustum	Moss	-	0.7131	0.1266
Riccardia cochleata	Liverwort	3	**<0.0001**	**0.0013**
Lepidozia ulothrix	Liverwort	3	0.8804	**0.0348**
Zoopsis argentea	Liverwort	-	0.3917	0.1797
Achrophyllum dentatum	Moss	-	0.4758	0.3173
Ptychomnion aciculare	Moss	-	0.1059	0.1430
Rhizogonium distichum	Moss	-	0.3008	0.1572
Bazzania adnexa	Liverwort	-	0.4407	0.1572
Dicranoloma billarderi	Moss	3	0.0702	**0.0010**
Wijkia extenuata	Moss	-	0.2340	0.2530
Rhizogonium novae-hollandiae	Moss	3	0.7105	**0.0007**
Telaranea tridactylis	Liverwort	3	**0.0078**	**<0.0001**

3.6 Meso- and micro-environmental variables in relation to regenerating forest age and decay class

3.6.1 Temperature and vapour pressure deficit changes with regenerating forest age and miniseason

Average daily temperature at 4 pm for each miniseason had a similar trend over time for each regenerating forest age (Figure 3.21). The average daily 4 pm temperature was significantly different among all miniseasons ($P < 0.0001$) with summer having the highest daily 4 pm temperature and winter having the lowest. There was also a very strong difference among regenerating forest ages ($P < 0.0001$). The 8 year old forest was significantly different from all other forest ages and had the most variation in average daily 4 pm temperature. The 20 and 32 year old forests were also significantly different from each other, but not significantly different from the 43 year old forest. Average daily minimum temperature also was significantly different among miniseasons ($P < 0.0001$) and among regenerating forest ages ($P < 0.01$; Figure 3.22). The 20 year old forest was significantly different from all other forest ages. The 8 year old forest was significantly different from the 43 year old forest, and neither was significantly different from the 32 year old forest.

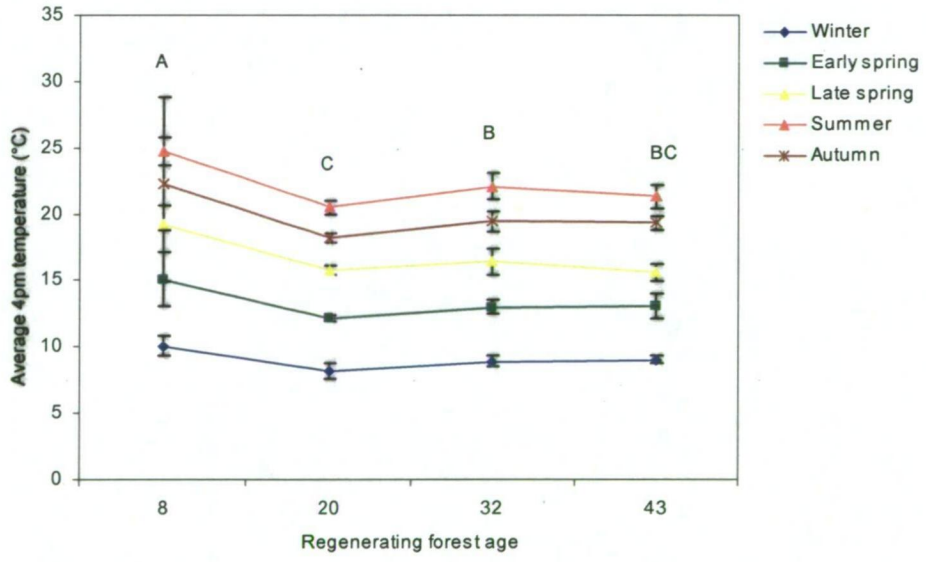

Figure 3.21. Average daily 4 pm temperatures per miniseason (± standard deviation) for each regenerating forest age. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed very highly significant differences among means for miniseason ($P < 0.0001$) and regenerating forest age ($P < 0.0001$). Letters above data points indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

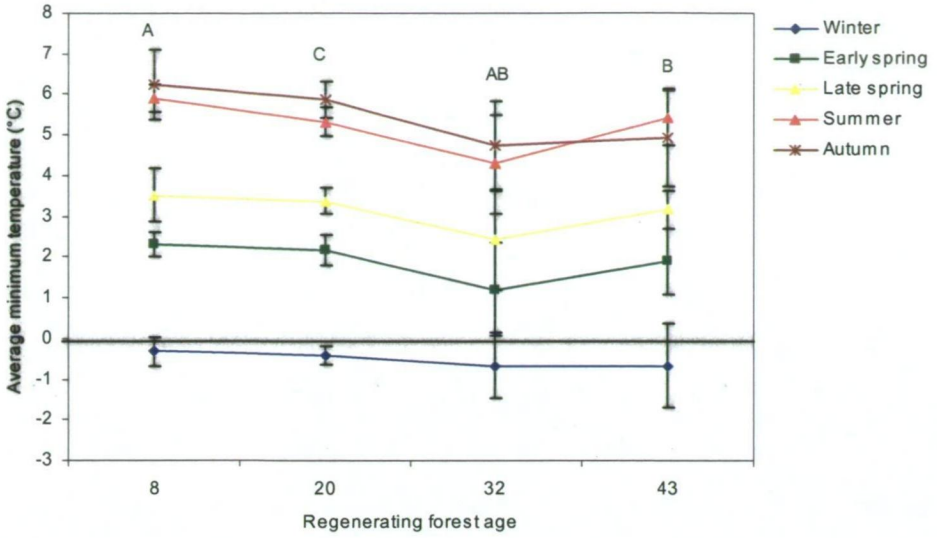

Figure 3.22. Average daily minimum temperatures per miniseason (± standard deviation) for each regenerating forest age. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed very highly significant differences among means for miniseason ($P < 0.0001$) and regenerating forest age ($P < 0.001$). Letters above data points indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

Average daily 4 pm vapour pressure deficit and average daily minimum vapour pressure deficit was variable among miniseasons and among regenerating forest ages (Figure 3.23 and 3.24). Average 4pm vapour pressure deficit was significantly different among miniseasons ($P < 0.0001$) and between regenerating forest ages, though the difference was less significant ($P < 0.01$). The 8 year old forest was significantly different to all other forest ages. There was no significant difference among the 20, 32 and 43 year old forests. Average daily minimum vapour pressure deficit was significantly different among miniseasons ($P < 0.0001$) and significantly different among regenerating forest ages ($P < 0.001$). The differences were the same between average 4pm daily vapour pressure deficit, where the 8 year old forest was significantly different from all other forest ages.

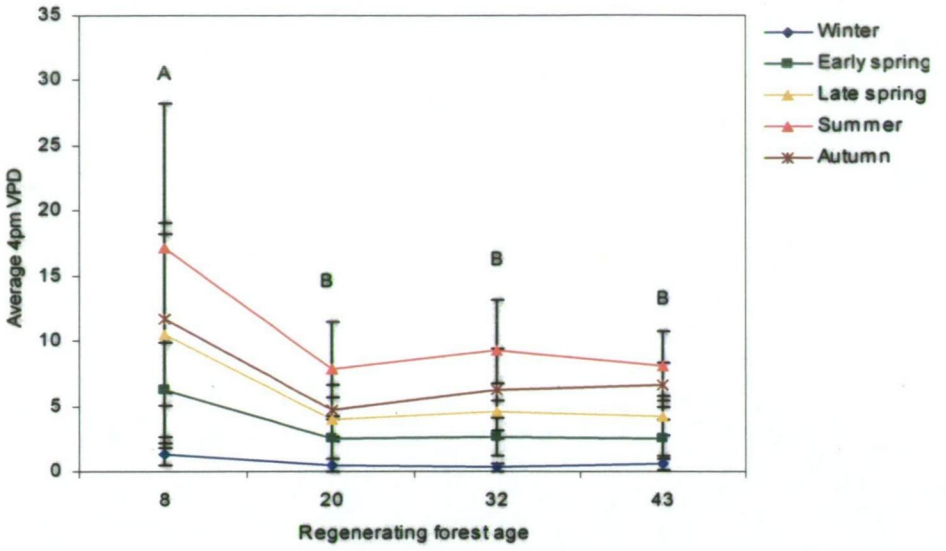

Figure 3.23. Average daily 4 pm vapour pressure deficit per miniseason (± standard deviation) for each regenerating forest age. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed very highly significant differences among means for miniseason ($P < 0.0001$) and regenerating forest age ($P < 0.01$). Letters above data points indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

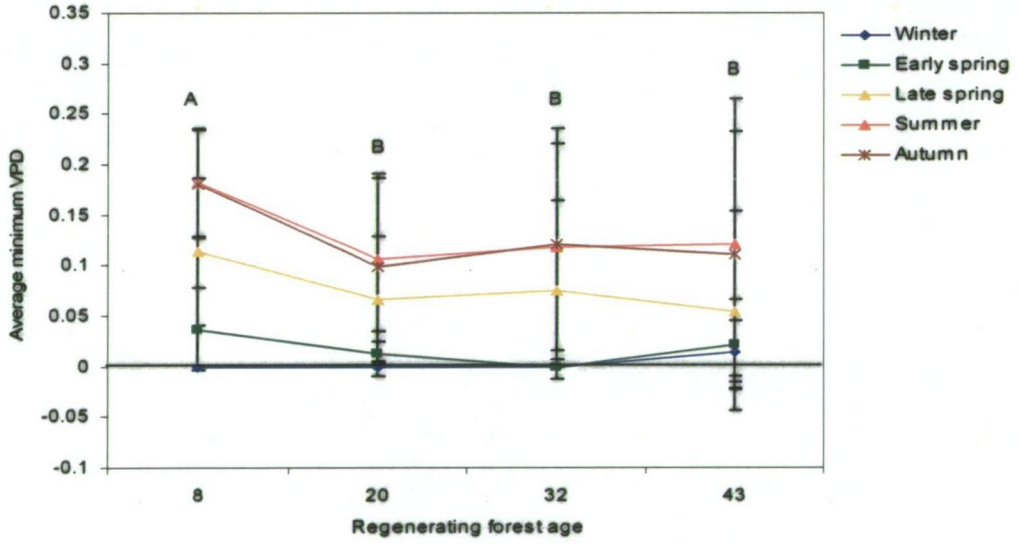

Figure 3.24. Average daily minimum vapour pressure deficit per miniseason (± standard deviation) for each regenerating forest age. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed very highly significant differences among means for miniseason ($P < 0.0001$) and regenerating forest age ($P < 0.001$). Letters above data points indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

3.6.2 Log moisture changes with regenerating forest age and decay stage

Log moisture increased significantly with increasing regenerating forest age ($P < 0.01$), from an average of 32.4% in the 8 year old regenerating forest up to 41.4% in the 43 year old regenerating forest based on the primary dataset, including all regenerating forest ages and decay classes (Figure 3.25).

Differences in average log moisture showed that the significant difference among decay classes was very strong ($P < 0.0001$) based on the primary dataset including all regenerating forest ages and decay classes (Figure 3.26). Decay class 2 had significantly lower log moisture than decay classes 3, 4 and 5, though the difference between decay class 2 and 5 was not significant; however, when the data was restricted to decay class 3 logs, log moisture was almost identical among regenerating forest ages 20, 32 and 43 (~39 - 40%) (Figure 3.27).

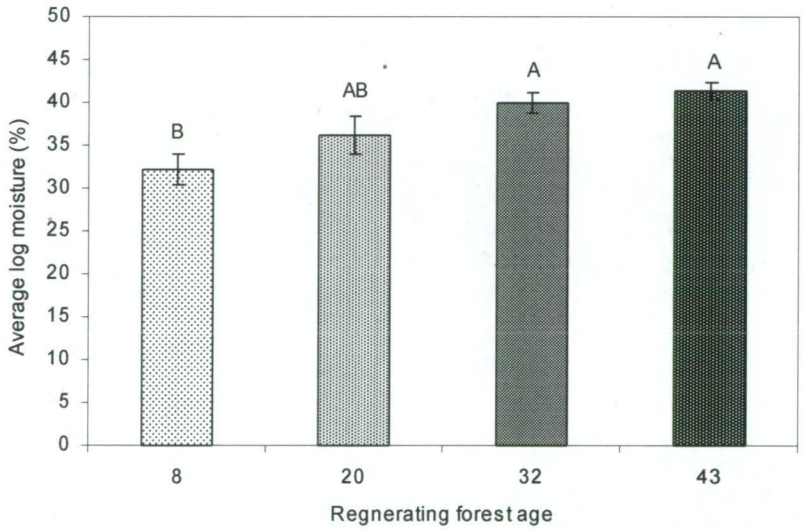

Figure 3.25. Average moisture on logs (% ± standard error) for each regenerating forest age. Averages are of two sampling events and three measures of per log per site. Values are from the primary dataset including all regenerating forest ages and decay classes. Analysis of variance showed significant differences among means ($P < 0.01$). Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

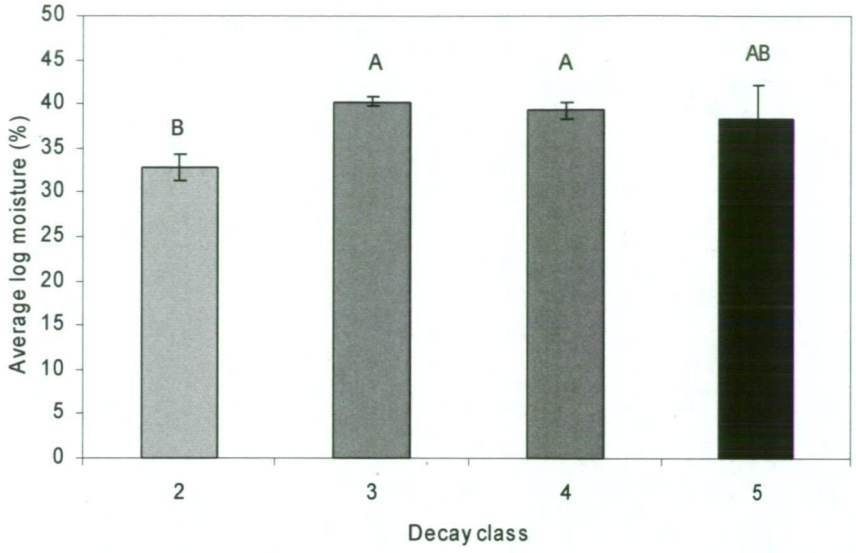

Figure 3.26. Average moisture on logs (% ± standard error) for each decay class. Averages are of two sampling events and three measures of moisture per log per site. Values are from the primary dataset including all forest ages and decay classes. Analysis of variance showed significant differences among means ($P < 0.0001$). Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

Figure 3.27. Average moisture on logs (% ± standard error) for each regenerating forest age. Averages are of two sampling events and three measures of moisture per log per site. Values are from the secondary dataset including the regenerating forest ages 20, 32 and 43 on logs of decay class 3. Analysis of variance showed no significant differences among means ($P > 0.05$). Letters above the columns indicate results of post-hoc tests - columns sharing a letter are not significantly different ($P > 0.05$).

Decay classes 3 logs showed considerably higher mean moisture than decay class 2 logs within the 20 year regenerating forest age class ($P < 0.05$; Figure 3.28).

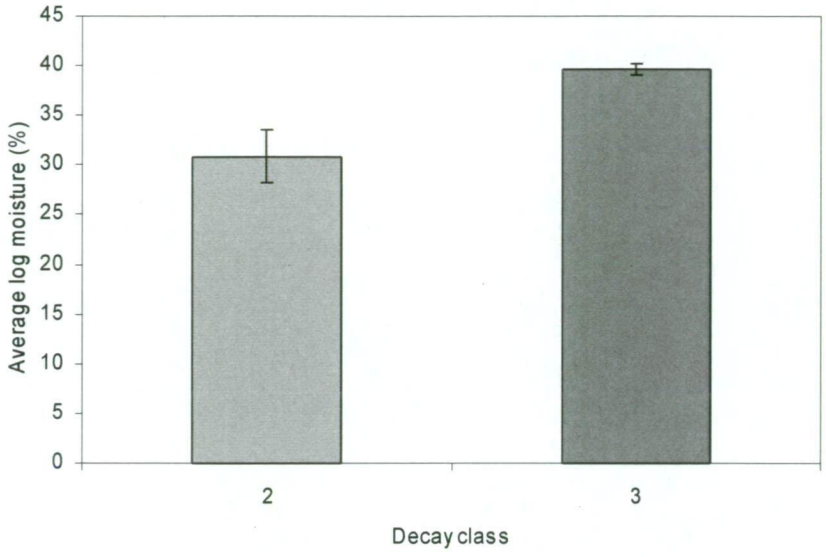

Figure 3.28. Average moisture on logs (% ± standard error) for each decay class. Averages are of two sampling events and three measures of moisture per log per site. Values are from the secondary dataset including decay classes 2 and 3 within the 20 year old regenerating forest. Analysis of variance showed significant differences among means ($P < 0.05$).

3.6.3 Individual species associations with regenerating forest age and decay stage in relation to log moisture

Individual species analysis of percentage cover comparing forest ages with log moisture as a covariate, using the primary dataset including all regenerating forest ages and decay classes, detected a significant log moisture association with time since disturbance for only one species (Table 3.8). The moss *Rhizogonium novae-hollandiae* was significantly associated with increasing log moisture but also with increasing forest age.

Table 3.8. Significance of the covariate log moisture and fixed effect forest age (probability associated with moisture as a covariate in REML analyses with forest age as a fixed effect and site within age as a random effect) for percentage cover of individual species in the primary dataset including all regenerating forest ages and decay classes. Species chosen occurred on more than 9% of the 220 logs sampled. Values in bold are significant.

Species	Taxonomic group	Log moisture (*P*)	Forest age (*P*)
Chiloscyphus semiteres	Liverwort	0.4716	0.6035
Cephaloziella hirta	Liverwort	0.6860	**0.0034**
Cephaloziella exiliflora	Liverwort	0.0643	**0.0005**
Campylopus introflexus	Moss	0.4973	**0.0246**
Riccardia crassa	Liverwort	0.0796	**0.0360**
Dicranoloma robustum	Moss	0.4138	0.5833
Riccardia cochleata	Liverwort	0.1881	0.3974
Lepidozia ulothrix	Liverwort	0.9223	0.1445
Zoopsis argentea	Liverwort	0.1238	**0.0081**
Achrophyllum dentatum	Moss	0.7472	0.6303
Ptychomnion aciculare	Moss	0.0518	0.2723
Rhizogonium distichum	Moss	0.0753	**0.0385**
Bazzania adnexa	Liverwort	0.7373	**0.0050**
Dicranoloma billarderi	Moss	0.8680	**0.0461**
Wijkia extenuata	Moss	0.1406	**0.0160**
Rhizogonium novae-hollandiae	Moss	**0.0052**	**<0.0001**
Telaranea tridactylis	Liverwort	0.0747	**0.0024**

Individual species analysis of log moisture as a covariate with either forest age or log decay as independent variables for the secondary datasets of: (1) forest age independent of decay class including the forest ages 20, 32 and 43 on logs of decay class 3 only; and (2) decay class independent of forest age including decay classes 2 and 3 on the 20 year old forest only showed that log moisture was a significant covariate with either forest age or decay class for only a few species (Table 3.9). The independent effect of forest age with log moisture as a covariate was significant for the moss *Rhizogonium novae-hollandiae* and the liverworts *Cephaloziella exiliflora, Zoopsis argentea* and *Telaranea tridactylis.* This result for *Cephaloziella exiliflora, Rhizogonium novae-hollandiae* and *Telaranea tridactylis* was similar to the result from the primary dataset of all forest ages and decay classes. However, *Zoopsis argentea* was not significantly associated with log moisture and forest age based on forest age independent of decay class. The independent effect of decay class with log moisture as a covariate was significant for the covariate log moisture for the liverwort *Telaranea tridactylis.*

Table 3.9. Probability of log moisture effect as a covariate in REML analyses with forest age or decay class as a fixed effect and site within age as a random effect. (1) Analysis of percentage cover of individual species from the secondary dataset of forest age independent of decay class including the forest ages 20, 32 and 43 on logs of decay class 3. (2) Analysis of percentage cover of individual species from the secondary dataset of decay class independent of forest age including decay classes 2 and 3 on the 20 year old forest. Species chosen occurred on more than 9% of the 220 logs sampled. Values in bold are significant.

		(1) Forest age		(2) Decay class	
Species	Taxonomic group	Log moisture (*P*)	Forest age (*P*)	Log moisture (*P*)	Decay class (*P*)
Chiloscyphus semiteres	Liverwort	0.7025	0.8853	0.4987	0.5211
Cephaloziella hirta	Liverwort	0.2124	**0.0208**	0.8216	0.6212
Cephaloziella exiliflora	Liverwort	**0.0040**	**0.0158**	0.6934	0.9793
Campylopus introflexus	Moss	0.8337	0.0676	0.8556	0.5076
Riccardia crassa	Liverwort	0.3634	**0.0308**	0.1491	0.5898
Dicranoloma robustum	Moss	0.1149	0.5068	0.3286	0.9010
Riccardia cochleata	Liverwort	0.5770	**0.0142**	0.7967	0.8480
Lepidozia ulothrix	Liverwort	0.4555	0.3486	0.5388	0.1121
Zoopsis argentea	Liverwort	**0.0316**	0.3017	0.7606	0.1301
Achrophyllum dentatum	Moss	0.1152	0.8430	0.8570	0.3915
Ptychomnion aciculare	Moss	0.7441	0.3243	0.2875	**0.0130**
Rhizogonium distichum	Moss	0.3570	0.0960	0.9141	0.8996
Bazzania adnexa	Liverwort	0.8832	0.1464	0.9596	0.4155
Dicranoloma billarderi	Moss	0.0554	**0.0239**	0.8732	0.9806
Wijkia extenuata	Moss	0.2471	**0.0296**	0.7032	0.5369
Rhizogonium novae-hollandiae	Moss	**0.0089**	**0.0357**	0.5931	0.7115
Telaranea tridactylis	Liverwort	**0.0057**	**0.0009**	**0.0203**	0.5629

4. DISCUSSION

The present study considers how species richness and composition of cryptogams change in forests regenerating after clearfell, burn and sow silviculture. These changes could be the result of several processes, and the combination of these processes will be considered based on the association of these changes with changes in the nature of the substrate and mesoclimate. One scenario is that succession could be the accumulation of species based on their dispersal ability, in which case the expected result would be that there was no relationship between succession and substrate or mesoclimate variables, and early arriving species would not decline in abundance over time. On the other hand it could be the result of succession on the substrate, in which case there should be clear differences between log decay classes within the same forest age. It could also be related to changes in mesoclimate as the forest ages. Each of these alternatives will be considered below.

4.1 Overall community changes with time

As hypothesised, there were significant changes in community composition with forest age. The 8 and 43 year old forests were very distinct in their community composition, whereas the 20 and 32 year old forests were most similar in their species composition (Figure 3.3). Worldwide, studies have found that change in community composition is a key factor in defining cryptogam community succession on coarse woody debris (Ashton 1986; Crites and Dale 1998; Rambo and Muir 1998).

Also as was proposed, species richness increased significantly over time. This increase was significant between the 8 and 43 year old forests and although it was not independent of log diameter, results still showed a strong relationship for species richness over time when log diameter was included as a covariate. Log diameter is known to be associated with cryptogam species richness on coarse woody debris and may have influenced results due to increased sample sizes on larger logs in older forests (Kruys *et al.* 1999). The overall increase in species richness is consistent with other studies on coarse woody debris that indicate that time since disturbance is an important influence on cryptogam community succession. Rambo and Muir (1998), in a study on bryophyte species associations with coarse woody debris and forest age, found that the average species richness of bryophytes was greater in old forests than young forests.

Mosses, liverworts and ferns have different patterns of increasing species richness over time. For the moss and liverwort groups, the 43 year old forest had significantly higher

species richness than younger regenerating forest. However, the rate of increase in moss species richness over time was approximately twice that of liverworts. Liverwort species richness is commonly known to increase over time and be high in old forests (Crites and Dale 1998; Muhle and LeBlank 1975; Söderström 1988b). The increase in liverwort species in the older forest compared to the younger forest is consistent with findings from these studies.

The evidence of species specificity for successional age of the forest was clear, where all but one of the most common species (occurring on more than 9% of logs), had specific associations with a particular forest age. Most of these were associated with the later successional stages, but several early and mid successional species were identified. The only exception was the common liverwort *Chiloscyphus semiteres*, which did not have any significant associations with forest age. This species was commonly found in wet eucalypt forests of a similar age to this study by Turner (2003) when examining individual species substrate and age associations, and was found to have significant associations with coarse woody debris in forest aged 33 - 67 years. Different associations found in that study compared to the present study may be due to differences in analysis and sampling intensity, forest type and disturbance history, because each of these variables can change the interpretation of results.

Early successional species were deemed to be those with significant associations with the 8 year old regenerating forest. They included the liverworts *Cephaloziella hirta*, *Cephaloziella exiliflora*, and the moss *Campylopus introflexus*. One of these species, *Cephaloziella exiliflora*, was identified previously as an early successional species, being present on logs in clearfelled coupes in the same region as the present study three years after the regeneration burn (Duncan and Dalton 1982). The species identified in that study as the primary terrestrial colonisers, *Marchantia berteroana*, *Funaria hygrometrica, Ceratodon purpureus*, and *Polytrichum juniperinum* (all of which, although they were most common as ground mosses, were observed as present on logs one year following the burn) were not detected on logs after 8 years of regeneration in the present study.

Mid successional species were those species significantly associated with either the 20 or 32 year old regenerating forest. These included the liverworts *Riccardia crassa* and *Riccardia cochleata*, and the moss *Dicranoloma robustum*. Interestingly, *Riccardia crassa* increased in abundance at the same time as *Cephaloziella hirta* and *Campylopus introflexus* appeared to drop out of the community. *Cephaloziella exiliflora* maintained its

abundance until it dropped out in the 32 year old forest, when *Riccardia cochleata* and *Dicranoloma robustum* were at their peak in abundance.

More than half of the most common species found in this study were classified as late successional species as they were associated strongly with the 43 year old regenerating forest. These included the four most abundant and frequently occurring species, the mosses *Wijkia extenuata*, *Rhizogonium novae-hollandiae*, and *Dicranoloma billarderi* and the liverwort *Telaranea tridactylis*. These species are known to be common on logs in 60 year old wet eucalypt forests from another study in the same area (Jarman and Kantvilas 2001). Thus, the relative frequency of individual species in the present study is consistent with the findings from other studies in wet eucalypt forests in the same area. All of the species that were significantly associated with the 43 year old forest were also present in the cryptogam community on coarse woody debris after 32 years.

Overall, it is apparent that the distinction in community composition, or lack thereof, between forest ages can be best understood from the individual species scale. Where there was a clear distinction between forest ages 8 and 43 this was evident in there being no overlap in individual species associations between these forest ages, and where there was little distinction between the 20 and 32 year old forests there was a lot of similarity in the species that occurred in these forest ages.

In addition, the current study combined with Duncan and Dalton's (1982) earlier work establishes a clear successional pattern on logs post clearfelling. It is possible that many of the other species found in the present study have specific associations with forest age, but sampling intensity was not sufficient to identify these associations. Further investigation into these relationships may not provide substantial additional insight into successional processes on coarse woody debris because it is likely that the overall processes identified in the present study for species are also indicative of the successional relationships of other species.

The pattern of species replacement with succession in the present study is quite different from the patterns observed in general studies of succession following natural disturbance on coarse woody debris in the northern hemisphere, where the succession often is defined by four distinct successional stages characterised by functional groups, starting with epiphytic bryophytes and ending with terrestrial bryophytes (Crites and Dale 1998; Rambo and Muir 1998; Söderström 1988a). These distinct differences in succession between those

found in this study and those found in the northern hemisphere may be directly related to the nature of the disturbance that began succession on the log which determines the starting point of the cryptogam community, a factor which has been identified as important in determining the subsequent pattern of succession (Noble and Slatyer 1980). In northern hemisphere studies on succession following clear cut harvesting, it is recognised that cryptogam diversity increases over time (Newmaster and Bell 2002; Rudolphi 2007). Thus, in spite of the lack of distinct successional stages, the findings in the present study are consistent in these ways with successional patterns from similar clearfell, burn and sow disturbance types in forested systems worldwide.

4.2 Habitat changes

The process of succession can be best understood by considering the changes in habitat components with time. This is particularly important given that the aging of the regenerating forest includes a range of processes, including the aging of the substrate and changes in forest structure (Specht and Specht 1993) with consequent effects on meso- and microclimate.

The large variation in distribution of log decay classes within forest age (Table 2.3) is likely to be the result of log decay progressing over time as the forest ages. This results in mixed distributions of decay classes in particular forest ages after clearfell harvesting. These unique combinations of decay class and forest age over time have distinct effects on the composition of cryptogam communities on coarse woody debris and are a major component of the complexity of habitat change over time that determines the nature of succession.

There is clear evidence that mesoclimate varied with forest age, with average daily 4pm temperature and average daily 4pm vapour pressure deficit decreasing with forest age (Figures 3.21 and 3.23).This is consistent with the findings of other studies of variation in mesoclimate between forest ages. Crites and Dale (1998), in a study on bryophyte species distribution in relation to forest habitat changes over time, suggest that time since disturbance affects microclimate conditions. Other studies have also identified temperature and vapour pressure deficit and variation within these, as being directly related to forest age (Chen *et al.* 1999; Fenton and Frego 2005).

This fact that log moisture increased among decay class 2 and decay classes 3 and 4 both overall and independent of age suggests that the increasing log moisture with forest age

were largely the result of the differences in log moisture among log decay class. Log moisture is well known to be associated with decay class (Rambo 2001; Rambo and Muir 1998). However, it could not be determined if log decay class had an additional effect on mesoclimate differences between forest ages and whether this contributed to differences in site moisture. It is possible that higher evaporation rate in the younger forests than older forests as indicated by higher vapour pressure deficit (Figure 3.23) influenced log moisture in these forest ages. Also, advanced decay classes with high log moisture are better able to contribute to a more equable and humid mesoclimate (Rambo 2001), and consequently also contribute to differences in microclimate conditions.

4.3 The effects of habitat changes on cryptogamic land plant communities

CAP analysis (Figure 3.20) suggested that forest age was a more important determinant of the community composition than log decay class. This was supported to a degree by the analyses of the two independent data sets, although it must be recognised that these data sets covered smaller ranges of the age parameters than the overall data set (i.e. the data set testing the independent effect of age included only the 20, 32 and 43 age classes in decay class 3, and the data set testing the independent effect of decay class only included decay classes 2 and 3 in the 20 year age class). As a result, these analyses may have failed to detect changes that would be evident in broader samples. The significant preference of liverworts *Cephaloziella hirta, Cephaloziella exiliflora* and *Riccardia crassa* for 20 year old forest over older forest ages emphasises their status as early or mid successional species. The consistently significant preference of the mosses, *Achrophyllum dentatum, Ptychomnion aciculare, Rhizogonium distichum, Dicranoloma billarderi, Wijkia extenuata* and *Rhizogonium novae-hollandiae*; and the liverworts, *Zoopsis argentea, Bazzania adnexa* and *Telaranea tridactylis*, for the 43 year old forest over younger forest ages, emphasises their status as late successional species. The significantly higher species percentage cover in the 43 year old forest than the 20 and 32 year old forests can be attributed mainly to the number of liverwort species, a result that further supports the association between liverworts and older forests.

However, changes in associations with forest age for some species suggests that these species may be more strongly associated with habitat variables other than forest age. Thus, the liverwort *Lepidozia ulothrix* and the mosses *Campylopus introflexus, Dicranoloma robustum* and *Dicranoloma robustum* did not have any significant associations with forest

age independent of decay class, even though the overall data showed significant associations with particular forest ages.

The independent effect of decay class on the community was characterised by an increase in species richness and changes community composition. Some individual species show significant associations with a decay class, for example *Cephaloziella exiliflora* was the only species to be significantly associated with logs of decay class 2, and the liverworts *Chiloscyphus semiteres, Riccardia crassa, Riccardia cochleata, Lepidozia ulothrix* and *Telaranea tridactylis*, and the mosses *Dicranoloma billarderi* and *Rhizogonium novae-hollandiae* had significant associations with logs of decay class 3. This is consistent with other studies that also found a higher number of species associated with more advanced stages of decay than earlier stages of decay (Crites and Dale 1998; Kruys *et al.* 1999), and shows that there is a strong relationship between species composition and decay class.

Overall, these comparisons indicate that both the age of the regenerating forests and the age of the logs contribute to succession on coarse woody debris. However, there are indications that the forest age alone is more significant.

There is clear evidence for associations between cryptogam community succession and habitat conditions. These associations further demonstrate the complexity of the interactions between habitat and communities. For example, forest age had a significant effect on cryptogam community succession when analysed inclusive of decay class. Changes in mesoclimate and increasing log moisture may have been contributing factors in the increase in species richness over time and the greater number of individual species that had significant associations with the 43 year old forest than with younger forests. The findings of other studies suggest that moist, protected forest microclimates support the most diverse and abundant bryophyte communities (Andersson and Hytteborn 1991; Rambo and Muir 1998; Söderström 1988b). Thus, the observed relationships between mesoclimate and cryptogam communities in the present study are consistent with those from other forest systems and the interaction between mesoclimate and log moisture is very important in determining cryptogam species distribution and abundance over time.

4.4 Comparing clearfell, burn and sow and natural wildfire regeneration

The assessment of whether cryptogamic land plant succession after clearfell, burn and sow is similar to succession after wildfire, and also the comparison between clearfell, burn and sow and wildfire regeneration provides evidence that indicates how close 43 year old

clearfell, burn and sow regeneration is to the near climax state exhibited in old growth forest. Old growth forest refers to old stands (>110 years) of mixed forest with a predominantly rainforest understorey without any signs of natural or man made disturbance (Browning 2006; Turner 2003). This can be done by comparing the present data with data from an earlier study (Browning 2006). Browning (2006) and the present study were in the same region and sampling times differed by only two years (2006 versus 2008) but they differed in how the logs were sampled. Browning (2006) sampled decay class 3 logs, and assessed cover/abundance on three 20 cm^2 quadrats on each log; however, an unbiased comparison was made between the two studies by converting individual Braun-Blanquet scores for each species to percentage covers (as described in section 2.3.6), then calculating the means of these scores for each site. It should be noted that while percentage cover per log was comparable, these results did not provide an accurate representation of the relative species richness in each forest type as would be seen based on species richness if the studies had the same sampling intensities.

Approximately 55% of species are shared between the clearfell, burn and sow and the wildfire regenerating forests after 43 years (Table 4.1). The main differences were that the mosses *Wijkia extenuata*, *Dicranoloma menziesii* and *Distichophyllum pulchellum* had significantly higher percentage cover per log in the 43 year old wildfire regenerating forests than the 43 year old clearfell, burn and sow regenerating forest. Nine out of 69 species were present in the 43 year old wildfire regenerating forest but do not occur in the 43 year old clearfell, burn and sow regenerating forest. These species were the liverworts *Trichocolea mollissima, Telaranea mooreana*; the mosses *Hypnodendron comosum, Dicranoloma menziesii, Plagiothecium lamprostachys* and *Fissidens oblongifolius*; and the ferns *Hymenophyllum australe, Hymenophyllum rarum* and *Tmesipteris obliqua*. The same fern species were found to be greatly reduced in frequency in clearfell, burn and sow regenerating forests in another Tasmanian study comparing clearfell, burn and sow and wildfire regeneration (Hickey 1994). These fern species that occur on standing dead trees initially as epiphytes were lost due to the loss of habitat refugia in clearfell, burn and sow regenerating forests compared to wildfire regenerating forests, which preserve many of these essential habitat elements. Eight out of 69 species are present in the 43 year old clearfell, burn and sow forest but did not occur in the wildfire regeneration forests: the liverworts *Chiloscyphus multipennus*, *Chiloscyphus latifolius* and *Kurzia compacta*; the mosses *Rhynchostegium tenuifolium* and *Rhaphidorrhynchium amoenum;* and the ferns

Hypolepis rugosula, Pteridium esculentum and *Polystichum proliferum* (Table 4.1). Although some of these differences may be the result of sampling limitations, the presence of significant differences in some species, plus the large number of other differences indicate that succession on coarse woody debris is different after wildfire than after clearfell, burn and sow. Similar differences in the composition of forests regenerating following wildfire and clearfell, burn and sow silviculture have been found previously (Turner 2003), and may reflect differences in how some bryophyte and fern species respond to wildfire and clearfell, burn and sow harvesting disturbance.

There were also differences between old growth forest and both the wildfire and clearfell, burn and sow regeneration at 43 years. Nine out of 69 species were significantly more abundant in the old growth than in the younger regeneration types based on REML analysis of the differences between the percentage cover per log of each species among forest types based on the same design as the present study. These were the mosses *Rhizogonium novae-hollandiae, Leucobryum candidum* and *Hypnum chrysogaster*; the liverworts *Zoopsis argentea, Tylimanthus diversifolius, Trichocolea mollissima* and *Heteroscyphus fissistipus*; and the ferns *Grammitis billardierei* and *Hymenophyllum rarum* (Figure 4.1). In addition the moss *Hypnodendron vitiense* and the liverworts *Bazzania monilinervis, Psiloclada clandestina, Plagiochila strombifolia, Marsupidium surculosum, Radula buccinifera, Riccardia eriocaula* and *Saccogynidium decurvum* only occurred in the old growth forest (Table 4.1). Many of these bryophytes also have been reported as common in other old growth forests in Tasmania (Turner 2003).

Table 4.1: Individual species presence in each forest type. Presence was based on percentage cover data only from the present study and Browning (2006).

		Forest type		
Species	Taxonomic group	Clearfell, burn and sow regeneration (43 years)	Wildfire regeneration (43 years)	Old growth (>110 years)
Blechnum wattsii	Fern	+	+	+
Grammitis billardierei	Fern	+	+	+
Hymenophyllum cupressiforme	Fern	+	+	+
Hymenophyllum flabellatum	Fern	+	+	+
Rumohra adiantiformis	Fern	+	+	+
Acromastigum colensoanum	Liverwort	+	+	+
Bazzania adnexa	Liverwort	+	+	+
Heteroscyphus biciliatus	Liverwort	+	+	+
Chiloscyphus semiteres	Liverwort	+	+	+
Gackstroemia weindorferi	Liverwort	+	+	+
Heteroscyphus coalitus	Liverwort	+	+	+
Heteroscyphus fissistipus	Liverwort	+	+	+
Hymenophyton flabellatum	Liverwort	+	+	+
Jamesoniella tasmanica	Liverwort	+	+	+
Lepidozia glaucophylla	Liverwort	+	+	+
Lepidozia laevifolia	Liverwort	+	+	+
Lepidozia ulothrix	Liverwort	+	+	+
Metzgeria furcata	Liverwort	+	+	+
Podomitrium phyllanthus	Liverwort	+	+	+
Riccardia cochleata	Liverwort	+	+	+
Riccardia crassa	Liverwort	+	+	+
Telaranea sp.	Liverwort	+	+	+
Tylimanthus pseudosaccatus	Liverwort	+	+	+
Tylimanthus diversifolius	Liverwort	+	+	+
Zoopsis argentea	Liverwort	+	+	+
Achrophyllum dentatum	Moss	+	+	+
Dicranoloma dicarpum	Moss	+	+	+
Dicranoloma billarderi	Moss	+	+	+
Distichophyllum pulchellum	Moss	+	+	+
Goniobryum subbasilare	Moss	+	+	+
Hypnum chrysogaster	Moss	+	+	+
Leptotheca gaudichaudii	Moss	+	+	+
Leucobryum candidum	Moss	+	+	+
Ptychomnion aciculare	Moss	+	+	+
Rhizogonium distichum	Moss	+	+	+
Rhizogonium novae-hollandiae	Moss	+	+	+
Thuidiopsis sparsa	Moss	+	+	+
Wijkia extenuata	Moss	+	+	+
Bazzania monilinervis	Liverwort			+
Marsupidium surculosum	Liverwort			+
Plagiochila strombifolia	Liverwort			+
Psiloclada clandestina	Liverwort			+
Radula buccinifera	Liverwort			+
Riccardia eriocaula	Liverwort			+
Saccogynidium decurvum	Liverwort			+

Zoopsis setulosa	Liverwort			+
Hypnodendron vitiense	Moss			+
Hymenophyllum australe	Fern		+	+
Hymenophyllum rarum	Fern		+	+
Tmesipteris obliqua	Fern		+	+
Trichocolea mollissima	Liverwort		+	+
Telaranea mooreana	Liverwort		+	+
Dicranoloma menziesii	Moss		+	+
Hypnodendron comosum	Moss		+	+
Cyanolophocolea echinella	Liverwort	+		+
Schistochila lehmanniana	Liverwort	+		+
Cyathophorum bulbosum	Moss	+		+
Dicranoloma robustum	Moss	+		+
Histiopteris incisa	Fern	+	+	
Fissidens oblongifolius	Moss		+	
Plagiothecium lamprostachys	Moss		+	
Hypolepis rugosula	Fern	+		
Polystichum proliferum	Fern	+		
Pteridium esculentum	Fern	+		
Chiloscyphus latifolius	Liverwort	+		
Chiloscyphus multipennus	Liverwort	+		
Kurzia compacta	Liverwort	+		
Rhaphidorrhynchium amoenum	Moss	+		
Rhynchostegium tenuifolium	Moss	+		

The liverwort *Zoopsis argentea* was the only species that had a significant association with the 43 year old clearfell, burn and sow regenerating forest and had significantly higher cover in the old growth forest. This species was found to be significantly associated with logs in both mature (between 33-67 years) and old growth forests (>110 years) in a previous study comparing substrate and forest age associations in wet eucalypt forests of Tasmania by Turner (2003). The species that were considered late successional in the 43 year old clearfell, burn and sow regenerating forest in the present study were not late successional species relative to old growth forest, except for the liverwort *Zoopsis argentea*. Consequently, it seems that species composition in the 43 year old clearfell, burn and sow regenerating forest has not reached the diversity or abundance of species found in old growth forest.

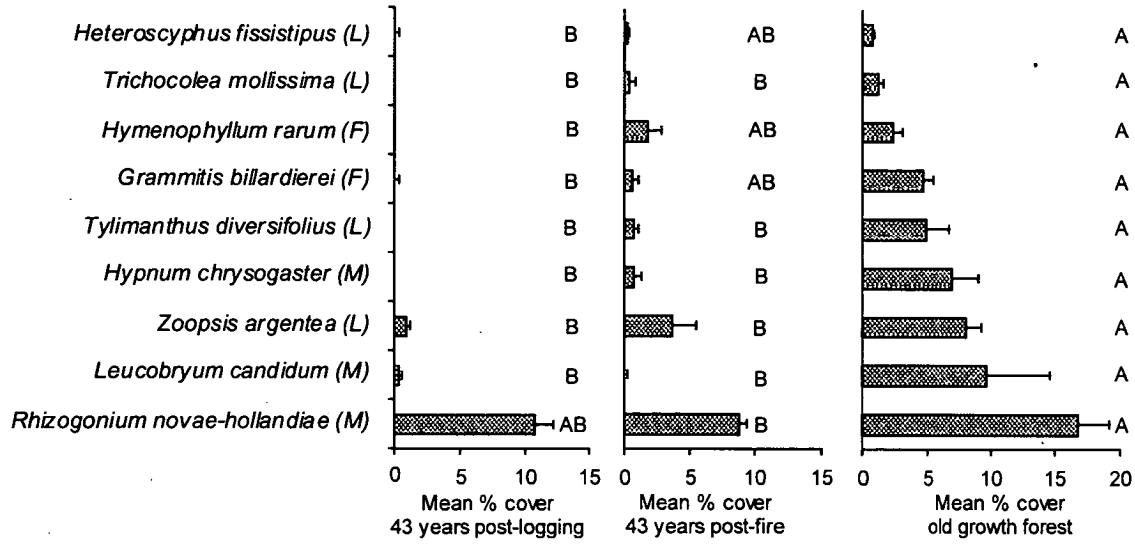

Figure 4.1. Average cover per log (± standard error) in different types of regenerating forest for species with a significant difference between forest types ($P < 0.05$). Post hoc tests comparing forest types are given - for each species forest types sharing a letter are not significantly different ($P > 0.05$). Abbreviations: M = moss, L = Liverwort, F = Fern.

The significant associations observed for forest age in the present study combined with observations from other studies reveal a distinct successional pattern for cryptogamic land plants on coarse woody debris. This succession is characterised by distinct early, middle, late and very late successional species (Table 4.2). However, while it is plausible that the 43 year old clearfell, burn and sow regenerating forest communities on coarse woody debris eventually will succeed to similar communities as observed in the old growth forest, it is possible this may be a more extended process than after wildfire, given the differences between the 43 year old post-wildfire and post-clearfell, burn and sow regeneration. However, it is also possible that the community of the old growth community that would succeed from the 43 year old clearfell, burn and sow regenerating forest could potentially be quite different from natural regeneration. This may include the loss of some of the species that were observed in the wildfire regenerating forest and the old growth forest that were not observed from the clearfell, burn and sow regenerating forest, especially those species dependent on particular habitat refugia to persist after stand-replacing disturbance. In the present study it was found that the combined effects of forest age and coarse woody debris habitat conditions largely determined the resulting cryptogam community in clearfell, burn and sow regenerating forests. It can be assumed that similar processes are

determining the succession of species after wildfire regeneration. Based on the difference in cryptogam communities between regeneration types 43 years after disturbance, some of these habitat conditions have been lost in the clearfell, burn and sow regenerating forests.

Table 4.2. Summary of the successional development of cryptogam communities on coarse woody debris in wet eucalypt forest after clearfell, burn and sow silviculture with the inclusion of old growth forest. Species included have significant associations with each forest age.

Time (years)	Successional stage	Characteristic species
8	Early	*Campylopus introflexus* (moss); *Cephaloziella hirta, Cephaloziella exiliflora* (liverworts)
20-32	Middle	*Dicranoloma robustum* (moss), *Riccardia cochleata, Riccardia crassa* (liverworts)
43	Late	*Achrophyllum dentatum, Dicranoloma billarderi Ptychomnion aciculare, Rhizogonium distichum, Rhizogonium novae-hollandiae, Wijkia extenuata* (mosses); *Bazzania adnexa, Telaranea tridactylis, Lepidozia ulothrix, Zoopsis argentea* (liverworts)
>110	Very late	*Hypnum chrysogaster, Leucobryum candidum, Rhizogonium novae-hollandiae* (mosses), *Heteroscyphus fissistipus, Tylimanthus diversifolius, Trichocolea mollissima, Zoopsis argentea* (liverworts), *Grammitis billardierei, Hymenophyllum rarum* (ferns)

4.5 Ecological and management implications

There needs to be a continuum of both decay classes and forest ages to ensure succession and the diversity of cryptogamic land plant assemblages over time on coarse woody debris. Variation in decay classes and associated habitat conditions is important for diversity and succession. In early successional forests, coarse woody debris, to a large extent, determines cryptogam community composition, which in turn determines the succeeding community that is observed in later successional forests. It is possible that there would be higher levels of species richness in early successional forests undergoing regeneration after clearfell, burn and sow harvesting if there was more variation in decay classes which have the potential to buffer cryptogam species microhabitat conditions and mediate some of the effect of the mesoclimate conditions in the early regenerating forests.

In the 43 year old clearfell, burn and sow regenerating forest it was the forest habitat that was indicated as limiting, not the decay classes and associated habitat conditions. Consequently, there is a need for forests older than 43 years after clearfell, burn and sow disturbance and a diversity of forest ages across the landscape. It is unlikely that the

proposed 100 year harvesting interval is enough for the progression of these communities to a point where community composition resembles those found in naturally regenerating mature or old growth forests (Grove *et al.* 2002; Hickey 1994). There is a large temporal gap from 43 year old clearfell, burn and sow regenerating forests to old growth forests, but even so, when comparing the two based on the comparative composition of the 43 year old wildfire regenerating forest, it would be fair to assume that these results provide a good indication of the state of successional regeneration and how closely related the clearfell, burn and sow regenerating forest is to natural regeneration. The present study suggests that because the clearfell, burn and sow community does not yet resemble naturally regenerating communities after 43 years, it may take longer than the proposed 100 years for the habitat elements, particularly important coarse woody debris elements such as standing dead trees, that serve initially as epiphytic habitat that were lost in the clearfell, burn and sow harvesting event to regenerate and time again to accommodate similar cryptogamic land plant communities. The establishment of very late successional species will take considerable time, and there is still time required after the establishment of those species for them to become similar in abundance, especially if the pattern of species succession in the younger clearfell, burn and sow regenerating forests is any indication, where species were present in the community for some time before becoming dominant. This means that there is the likely possibility that species will be excluded after repeat harvesting events of 100 year rotation. Therefore, conservation at a landscape level will depend on the distribution of essential habitat elements in the landscape in reserves as well as complementing management of these elements in multiple use forests such as through the wider use of variable retention harvesting.

There is a huge gap in knowing what is happening after 43 years in either clearfell, burn and sow regeneration and at what time these communities reach a stage where they compare to naturally regenerating and old growth communities. This information is still a long way off due to the absence of comparable clearfell, burn and sow coupes older than 43 years. This regeneration type is only available for forest approximately 43 years old because it was approximately 43 years ago that clearfell, burn and sow was implemented as a major harvesting technique (Wells and Hickey 1999). Therefore, longer rotation times (i.e. the times between subsequent harvests) are potentially required because the species that are significantly associated with the old growth forest are not even there yet, and it's likely that the habitat conditions for these species are only just developing, but will still take considerable time.

The present study suggests that there should be increased consideration for biodiversity on coarse woody debris, until there is further evidence for the successful regeneration of communities over the 100 year time frame. That means preserving old growth elements such as standing dead trees and large logs in various stages of decay in the managed landscape as much as possible, and ensuring that there is a mosaic of old growth and regenerating forests. The complexity of forest ages in the landscape will ensure that communities and species are not lost at a regional level even if they're lost at a site level (Fahrig 2001). The mosaic will increase the likelihood of reestablishment if it turns out that clearfell, burn and sow did not effectively resemble natural regeneration in accounting for coarse woody debris biodiversity. It is also important to encourage complexity in forest structure, including the maintenance of coarse woody debris in a continuum of decay classes and diameters to promote optimal diversity within any particular forest area and allow succession to occur without the restrictions that result from conventional clearfell, burn and sow harvesting (Grove *et al.* 2002). The potential implications of the present study support the conservation goals of many current and developing forest management prescriptions such as aggregated retention.

4.6 Conclusion

This study provides a significant contribution to understanding of how the dynamics of coarse woody debris and forest regeneration after clearfell, burn and sow relate to cryptogamic land plant succession on coarse woody debris. It provides clear evidence for the succession of cryptogamic land plant communities on coarse woody debris. This is characterised by changes in community composition and an increase in species richness over time, as well as the distinct replacement of species assemblages over time. The successional processes are driven by changes in forest habitat and coarse woody debris habitat, and these habitat changes co-vary with time since clearfell, burn and sow disturbance. The importance of each habitat scale in determining the succession of cryptogam communities is identified, as is the complexity of the interactions between these two habitat scales. It is recognised that there are potentially important community composition differences between clearfell, burn and sow and wildfire regeneration types. This information, coupled with the projected old growth community composition is cause for concern regarding the regeneration success of clearfell, burn and sow harvesting, and the important role of coarse woody debris in determining the success of cryptogam community development should not be underestimated. Management implications are that

both site and landscape level prescriptions may be needed to retain essential habitat elements and conservation goals in the wider forest landscape will require the retention of suitably diverse and abundant old growth elements.

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APPENDIX 1

MOSSES

Brachytheciaceae

Rhynchostegium tenuifolium (Hedw.) Reichardt

Bryaceae

Rosulabryum billarderi (Schwägr.) J.R.Spence

Dicranaceae

Dicranoloma billarderi (Brid. Ex Anon.) Paris

Dicranoloma dicarpum (Nees) Paris

Dicranoloma menziesii (Taylor) Renauld

Dicranoloma robustum (Hook.f. & Wilson) Paris

Fissidentaceae

Fissidens oblongifolius Hook.f. & Wilson

Hookeriaceae

Achrophyllum dentatum (Hook.f. & Wilson) Vitt & Crosby

Distichophyllum pulchellum (Hampe) Mitt.

Hypnaceae

Hypnum chrysogaster Müll.Hal.

Hypnodedraceae

Hypnodendron comosum (Labill.) Mitt.

Hypnodendron vitiense Mitt.

Hypopterygiaceae

Cyathophorum bulbosum (Hedw.) Müll.Hal.

Hypopterygium didictyon Müll.Hal.

Leptostomataceae

Leptostomum inclinans R.Br.

Leucobryaceae

Campylopus introflexus (Hedw.) Brid.

Leucobryum candidum (Brid. Ex P.Beauv.) Wilson

Mniaceae

Pohlia nutans (Hedw.) Lindb

Orthodontiaceae

Orthodontium lineare Schwägr.

Plagiotheciaceae

Plagiothecium lamprostachys (Brid. Ex P.Beauv.) Wilson

Polytrichaceae

Polytrichum juniperinum Hedw.

Ptychomniaceae

Ptychomnion aciculare (Brid.) Mitt

Racopilaceae

Racopilum cuspidigerum (Schwägr.) Ångstr.

Rhizogoniaceae

Goniobryum subbasilare (Hook.) Lindb.

Leptotheca gaudichaudii Schwägr.

Rhizogonium distichum (Sw.) Brid.

Rhizogonium novae-hollandiae (Brid.) Brid.

Splachnaceae

Tayloria gunnii (Wilson) J.H.Willis

Sematophyllaceae

Raphidorrhynchium amoenum (Hedw.) M.Fleisch.

Wijkia extenuata (Brid.) H.A.Crum

Thuidiaceae

Thuidiopsis sparsa (Hook.f. & Wilson) Broth.

LIVERWORTS

Acrobolbaceae

Marsupidium surculosum (Nees) Schiffn.

Tylimanthus diversifolius E.A.Hodgs.

Tylimanthus pseudosaccatus Grolle

Aneuraceae

Riccardia aequicellularis (Steph.) Hewson

Riccardia cochleata (Hook.f. & Taylor) Kuntze

Riccardia crassa (Schwaegr.) Carrington & Pearson

Riccardia eriocaula (Hook.) Besch. & C.Massal.

Cephaloziellaceae

Cephaloziella exiliflora (Taylor) Douin

Cephaloziella hirta (Steph.) R.M.Schust.

Geocalycacea

Chiloscyphus latifolius (Nees) J.J.Engel & R.M.Schust.

Chiloscyphus multipennus (Hook.f. & Taylor) J.J.Engel & R.M.Schust.

Chiloscyphus muricatus (Lehm.) J.J.Engel & R.M.Schust.

Chiloscyphus semiteres (Lehm. & Lindenb.) Lehm. & Lindenb.

Cyanolophocolea echinella (Lindenb. & Gottsche) R.M.Schust.

Heteroscyphus biciliatus (Hook.f. & Taylor) J.J.Engel

Heteroscyphus coalitus (Hook.) Schiffn.

Heteroscyphus fissistipus (Hook.f. & Taylor) Schiffn.

Saccogynidium decurvum (Mitt.)Grolle

Hymenophytaceae

Hymenophyton flabellatum (Labill.) Dumort. Ex Trevis.

Jungermanniaceae

Cuspidatula monodon (Taylor ex Lehm.) Steph.

Jamesoniella tasmanica (Hook.f. & Taylor) Steph.

Lepidolaenaceae

Gackstroemia weindorferi (Herzog) Grolle

Lepidoziaceae

Acromastigum mooreanum (Steph.) E.A.Hodgs.

Acromastigum colensoanum (Mitt.) A.Evans ex Reimers

Bazzania adnexa (Lehm. & Lindenb.) Trevis.

Bazzania monilinervis (Lehm. & Lindenb.) Trevis

Kurzia compacta (Steph.) Grolle

Lepidozia glaucophylla (Hook.f. & Taylor) Taylor ex Gottsche, Lindenb. & Nees

Lepidozia laevifolia (Hook.f. & Taylor) Taylor ex Gottsche, Lindenb. & Nees

Lepidozia ulothrix (Schwaegr.) Lindenb.

Psiloclada clandestina Mitt.

Telaranea herzogii (E.A.Hodgs.) E.A.Hodgs.
Telaranea mooreana (Steph.) R.M.Schust.
Telaranea tridactylis (Lehm. & Lindenb.) J.J.Engel & G.L.Merrill
Zoopsis argentea (Hook.f. & Taylor) Hook.f. ex Gottsche, Lindenb & Nees
Zoopsis setulosa Leitg.

Metzgeriaceae
Metzgeria furcata (L.) Dumort.

Pallaviciniaceae
Podomitrium phyllanthus (Hook.) Mitt.

Plagiochilaceae
Plagiochila strombifolia Taylor ex Lehm.

Radulaceae
Radula buccinifera (Hook.f. & Taylor) Taylor ex Gottsche, Lindenb. & Nees

Schistochilaceae
Schistochila lehmanniana (Lindenb.) Steph.

FERNS
Blechnaceae
Blechnum wattsii Tindale

Dennstaedtiaceae
Histiopteris incisa (Thunb.) J.Sm.
Hypolepis rugosula (Labill.) J.Sm.
Pteridium esculentum (G.Forst.) Cockayne

Dicksoniaceae
Dicksonia Antarctica Labill.

Dryopteridaceae
Polystichum proliferum (R.Br) C.Presl
Rumohra adiantiformis (G.Forst.) Ching

Grammitidaceae
Grammitis billardierei Willd.

Hymenophyllaceae

Hymenophyllum australe Willd.

Hymenophyllum cupressiforme Labill.

Hymenophyllum flabellatum Labill.

Hymenophyllum rarum R.Br.

Psilotaceae

Tmesipteris obliqua Chinnock